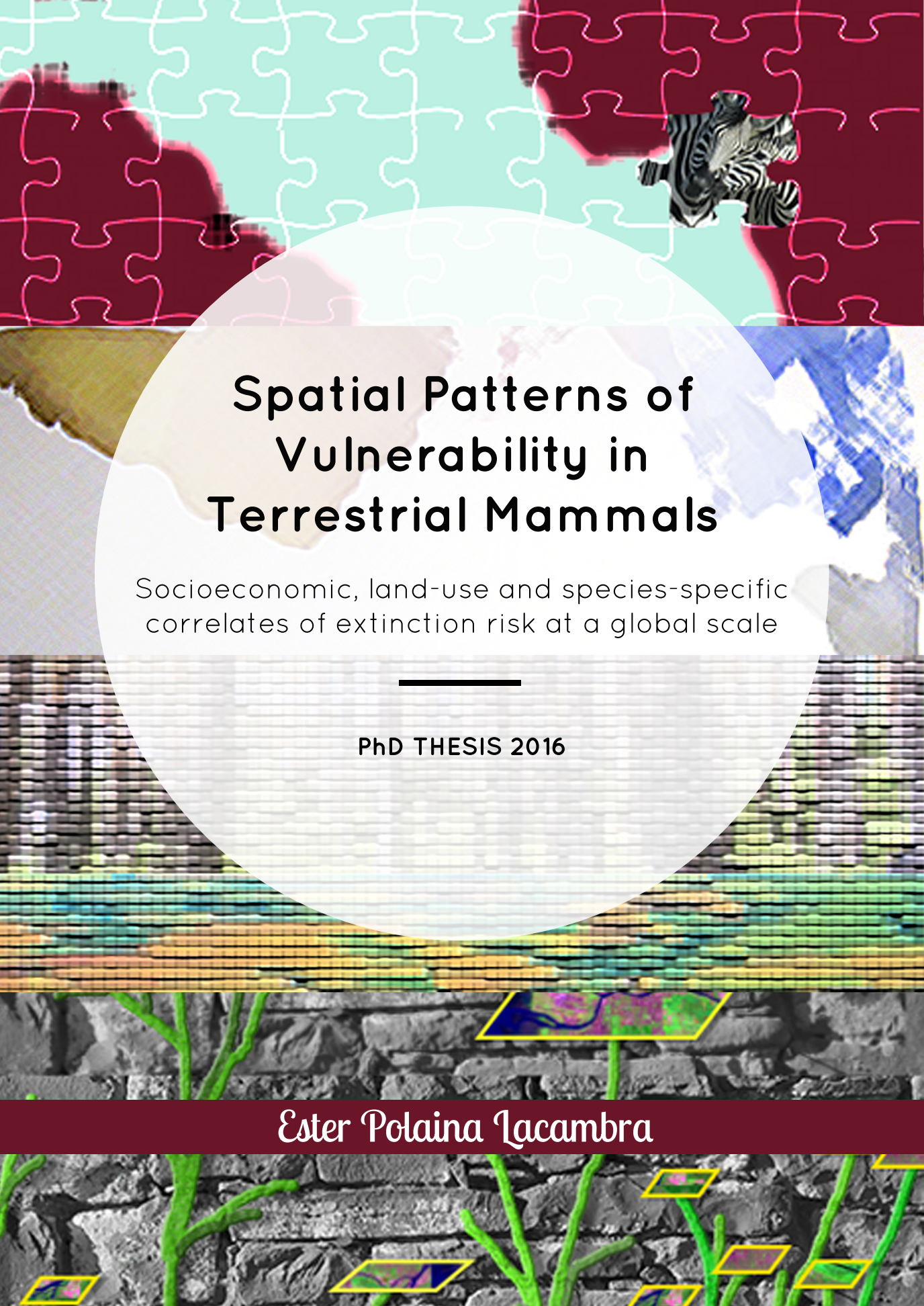

Spatial Patterns of Vulnerability in Terrestrial Mammals

Socioeconomic, land-use and species-specific correlates of extinction risk at a global scale

PhD THESIS 2016

Ester Polaina Lacambra

A las personas que hacen de este mundo un lugar mejor, a los que enseñan y a los que nunca dejan de aprender.

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Spatial Patterns of Vulnerability in Terrestrial Mammals

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Patrones Espaciales de Vulnerabilidad en Mamíferos Terrestres

Descriptores socioeconómicos, de uso del suelo y específicos de especie a escala global

Ester Polaina Lacambra

PhD Thesis

Sevilla, 2016

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Doctorado en Estudios Medioambientales

"**Spatial Patterns of Vulnerability in Terrestrial Mammals.** Socioeconomic, land use and species-specific correlates of extinction risk at a global scale"

Memoria presentada por la Licenciada en Ciencias Ambientales Ester Polaina Lacambra para optar al título de Doctor por la Universidad Pablo de Olavide

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CERTIFICAN

Que los trabajos de investigación desarrollados en la Memoria de Tesis Doctoral "Spatial Patterns of Vulnerability in Terrestrial Mammals. Socioeconomic, land use and species-specific correlates of extinction risk at a global scale" son aptos para ser presentados por la Licenciada Ester Polaina Lacambra ante el Tribunal que en su día se designe, para aspirar al Grado de Doctor por la Universidad Pablo de Olavide.

Y para que así conste, y en cumplimiento de las disposiciones legales vigentes, extendemos el presente certificado a 21 de junio de 2016.

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Fdo. Maria Luisa Buide del Real
Universidad Pablo de Olavide

In the end, it will be the appropriate management of people, not plants and animals, which determines the future state of our planet.

Gary Luck
Biological Reviews (2007)

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Summary

We are living an era of great and accelerated global changes. Biodiversity as a whole is exposed to human activities in the entire Earth surface and, as a consequence, a generalized deterioration of its conservation status is taking place. Besides, the impact of humans on the biosphere keeps increasing given the present demand for food, fuels and other natural resources, resulting from population and consumption growth. Understanding which species and areas are most affected by these activities, and which are the main drivers of their current status is a crucial step to avoid further damages and preserve some of the remaining natural values. In the present doctoral thesis I expand the concept of vulnerability to explore the distribution of extinction risk at a global scale. A vulnerable species is one that has a greater chance of becoming extinct given its intrinsic characteristics and the environmental conditions to which it is exposed. A vulnerable area is one that is more likely to disappear as such, given its combination of species and environmental (including human) features. The present thesis focuses on spatial vulnerability incorporating knowledge at the species level to improve our understanding of global changes. Terrestrial mammals are selected to investigate the different factors associated to vulnerability because they are a widely distributed and charismatic group for which information on intrinsic characteristics and main threats is largely available.

At the species level, predictors of vulnerability for terrestrial mammals have been widely identified. These can broadly be separated into species intrinsic traits and extrinsic human pressures. A spatial synthesis of both groups of factors is presented in Chapter 1, identifying areas where both intrinsic and extrinsic vulnerabilities present high values (*double-susceptibility* areas), areas where the intrinsic is high and the extrinsic is low (*intrinsic-susceptibility* areas), areas where the extrinsic is high and the intrinsic is low (*extrinsic-susceptibility* areas), and areas where both show relatively low values (*low-susceptibility* areas). Instead of prioritizing one type of areas over the others, specific conservation actions should be defined according to the particularities of each area. For example, in *extrinsic-susceptibility* areas the emphasis should be put

in controlling human activities, whereas in *intrinsic-susceptibility* areas, concentrating on particular species would be more advisable.

Subsequent chapters focus exclusively on spatial vulnerability, first exploring the socioeconomic context (Chapter 2) and then analyzing in depth the main proximate threat for mammals, human land use, explicitly considering its multiple facets (Chapters 3 and 4). A country's socioeconomic context has an important role in conservation biology, given that many indirect factors impose a global pressure on species and ecosystems (e.g. growth in world trade, demand for timber, etc.); besides, many environmental regulations are proposed at national –or international– level. Therefore, being able to portray the situation at this scale may serve to inform decision-making. Results from Chapter 2 show that countries harboring more threatened mammals are generally rural, predominantly exporters of goods and services, intermediately dependent on receiving international tourism and have relatively high human life expectancy. On the other hand, countries without threatened mammals are primarily those that already lost the most vulnerable fauna long ago and with means to maintain their remaining sensitive mammals. These findings highlight the importance of transboundary impacts and the fact that lack of threatened mammals is not necessarily a sign of good environmental conservation status.

Human land use is by far the main global change driver. There are many relevant aspects associated with its impact on biodiversity, such as land-use extent, intensity and history. Chapter 3 shows how including different metrics of agricultural land use and separating the world into regions with a historical and biogeographic common history can improve the understanding of the distribution of threatened species. Threatened mammals are not always found in zones where the most impacting human activities take place; instead, this pattern varies across biogeographic realms. Realms where agricultural expansion/intensification is currently taking place show a *refuge* pattern (e.g. Indomalay), with more threatened species concentrated in relatively low used areas (in terms of extent and/or intensity). On the other hand, regions with a long history of human settlement and a deeply modified

territory show a *threat* pattern (e.g. Europe), with more threatened mammals co-occurring in highly humanized areas.

Historical data offer the opportunity to learn lessons from the past that can inform present and future actions. Chapter 4 explores past land use data spanning from around B.C.6000 (~establishment of agriculture) to A.D.2000. These data reveal three different general types of regions in the world, based on their trajectory of land use: *low-*, *recently-* and *steadily-used* areas. These three groups do not present net differences in terms of mammalian diversity, but they do differ in the way past and present land-use metrics relate to total richness or numbers of threatened mammals. In general, indicators of past human land use extent and rate of changes are the most important predictors. Interestingly, present land use values are generally less relevant to explain global patterns of mammalian distribution than past land use.

In conclusion, looking at the different dimensions of human activities on Earth offers the necessary perspective to tackle global conservation problems. Together with the traditional approach of prioritizing areas that most deserve conservation funds, disentangling the particularities of each region –putting these areas into context– helps designing better conservation actions. This thesis synthesizes available global data, mapping patterns of threat for terrestrial mammals and proposing tools that could be applied to other taxonomic groups or drivers of extinction.

Resumen

Vivimos en una era de grandes y acelerados cambios globales. La biodiversidad en su conjunto se encuentra expuesta a actividades humanas a lo largo y ancho de la superficie terrestre y, como consecuencia, está teniendo lugar un deterioro generalizado de su estado de conservación. Además, el impacto humano en la biosfera sigue aumentando cada día debido a la actual demanda de alimentos, combustibles y otros recursos naturales, fruto del crecimiento poblacional y del consumo. Entender qué especies y áreas son las más afectadas por estas actividades, y cuáles son los principales ejes impulsores de su actual estado de conservación es un paso crucial para impedir mayores daños y preservar algunos de los valores naturales que aún quedan. En la presente tesis doctoral expando el concepto de vulnerabilidad con el objetivo de explorar la distribución del riesgo de extinción a escala global. Una especie vulnerable es aquella que tiene mayor probabilidad de extinguirse, dadas sus características intrínsecas y las condiciones ambientales a las que se encuentra expuesta. Un área vulnerable es aquella que tiene más opciones de desaparecer como tal, dadas su combinación de especies y características ambientales (incluyendo factores humanos). La presente tesis se centra en la vulnerabilidad espacial, incorporando el conocimiento a nivel de especie para mejorar nuestra comprensión de los cambios globales. Se han escogido los mamíferos terrestres para investigar los diferentes factores asociados a la vulnerabilidad porque son carismáticos y se distribuyen ampliamente; además existe información sobre sus principales rasgos intrínsecos y las principales amenazas a las que se ven expuestos.

A nivel de especie, los principales predictores de vulnerabilidad en mamíferos terrestres son conocidos; éstos pueden dividirse de manera genérica en: rasgos intrínsecos de especie, y presiones humanas externas. En el capítulo 1, se presenta una síntesis espacial de ambos grupos de factores, identificando áreas donde tanto la vulnerabilidad intrínseca como la extrínseca presentan valores altos (áreas de *doble susceptibilidad*), áreas donde la intrínseca es alta y la extrínseca baja (áreas de *susceptibilidad intrínseca*), áreas donde la extrínseca es alta y la intrínseca baja (áreas de *susceptibilidad extrínseca*), y áreas donde ambas presentan valores relativamente

bajos (áreas de *baja susceptibilidad*). En lugar de priorizar un tipo de áreas frente al resto, se propone definir acciones de conservación específicas acordes a las particularidades de cada área. Por ejemplo, en áreas de *susceptibilidad extrínseca* el énfasis debería ponerse en controlar las actividades humanas, mientras que en áreas de *susceptibilidad intrínseca* sería recomendable concentrarse en el manejo de especies concretas.

Los siguientes capítulos se centran exclusivamente en la vulnerabilidad a nivel espacial, primero explorando el contexto socioeconómico (Capítulo 2) y después analizando en profundidad la principal amenaza directa para los mamíferos: el uso del suelo por parte de los humanos, considerando de manera explícita sus múltiples facetas (Capítulos 3 y 4). El contexto socioeconómico de un país tiene un papel importante en biología de la conservación, ya que muchos factores indirectos imponen una presión global sobre las especies y los ecosistemas (ej. el crecimiento del comercio global, la demanda de madera, etc.); además, muchas regulaciones medioambientales se proponen a nivel nacional, o incluso internacional. Por tanto, ser capaces de retratar la situación a esta escala puede servir para informar la toma de decisiones. Los resultados del capítulo 2 muestran que los países que contienen más mamíferos amenazados son rurales, predominantemente exportadores de bienes y servicios, moderadamente dependientes del turismo internacional, y con una esperanza de vida relativamente alta. Por otro lado, los países sin especies amenazadas son principalmente aquellos que las perdieron tiempo atrás, y con medios para mantener aquellas especies sensibles que aún quedan dentro de sus fronteras. Estos hallazgos destacan la importancia de los impactos transfronterizos y el hecho de que no tener mamíferos amenazados no es necesariamente un signo de buen estado de conservación ambiental.

El uso del suelo humano es, con diferencia, el principal impulsor del cambio global. Existen muchos aspectos relevantes que se asocian con su impacto en la biodiversidad, tales como la extensión, la intensidad y la historia de uso. El capítulo 3 muestra cómo la inclusión de diferentes métricos de uso del suelo agrícola y la separación de regiones del mundo en base a su historia humana y biogeográfica puede ayudar a entender la actual distribución de especies amenazadas. Los mamíferos

amenazados no se encuentran siempre en zonas donde existen actividades humanas más impactantes, sino que este patrón varía entre regiones biogeográficas. Aquellas regiones en las que la expansión/intensificación agrícola está teniendo lugar en la actualidad muestran un patrón de *refugio* (ej. Indomalayo), con más especies amenazadas localizadas en áreas relativamente poco usadas (en términos de extensión y/o intensidad). Por otro lado, regiones con una larga historia de asentamiento humano y un territorio profundamente modificado muestran un patrón de *amenaza* (ej. Europa), donde más mamíferos amenazados coocurren con áreas más usadas por el ser humano.

Los datos de uso del suelo pasados ofrecen la oportunidad de aprender lecciones del pasado que pueden informar acciones presentes y futuras. El capítulo 4 explora algunos de estos datos, comprendidos entre aproximadamente el 6000 a.C. (~establecimiento de la agricultura) y el 2000 A.D. Estos datos revelan que el mundo puede separarse, esencialmente, en tres tipos de regiones en base a su trayectoria de uso del suelo: áreas *poco*, *recientemente* y *continuadamente* usadas. Estos tres grupos no presentan diferencias netas en términos de diversidad de mamíferos, pero difieren en el modo en que distintos métricos de uso del suelo pasado y presente se relacionan con la riqueza total de mamíferos y con el número de mamíferos amenazados. En general, el uso del suelo pasado y las tasas de cambio son los predictores más importantes. Curiosamente, los valores de uso del suelo actual son menos relevantes a la hora de explicar patrones globales de distribución de mamíferos que los datos de uso pasado.

En conclusión, explorar las distintas dimensiones de las actividades humanas sobre la tierra ofrece la perspectiva necesaria para hacer frente a los problemas de conservación globales. Junto a las aproximaciones tradicionales encaminadas a priorizar áreas más merecedoras de fondos para su conservación, desentrañar las particularidades de cada región (contextualizar) ayuda a diseñar mejor las acciones de conservación. Esta tesis sintetiza información disponible a escala global, mapeando patrones de amenaza en mamíferos terrestres, y proponiendo herramientas que podrían ser aplicadas a otros grupos taxonómicos y amenazas.

General introduction

While biodiversity declines, human pressure increases

Biodiversity loss is one of the crucial environmental concerns of the last decades. Increasing evidence shows that we are probably living a catastrophic era, entering the sixth mass extinction (Barnosky et al. 2012; Ceballos et al. 2015). It is not only about total species' extinctions, but also about how their decline at population level, produce further consequences on other elements of the environment. At local or regional scales, the local extirpation of a single species may trigger cascade effects on many others with complex interactions (Ripple et al. 2014; Pérez-Méndez et al. 2016). Defaunation and deforestation may also affect abiotic components of a system, such as water, air or soil, on which numerous species depend, including humans (Dirzo et al. 2014; Lewis et al. 2015). Still, we are only starting to understand the ecological consequences of local/regional extirpations, partly because responses may lag in time and partly because of the inherent uncertainties regarding complex ecological processes (Doak et al. 2008; Kuussaari et al. 2009). Nevertheless, some effects are well-described and widespread, including destabilization and loss of ecosystem functions (e.g. primary production, nutrient recycling, etc.; Cardinale et al. 2012).

But, how has biodiversity loss been assessed until now? Broadly, there are two main approaches. The first is demonstrating that extinction rates are greater than "background" rates –which in turn requires the estimation of those "background" extinction rates (Ceballos et al. 2015). The second consists of assuming different species-area relationships and then estimating the species that must have been lost according to the amount of depleted habitat (sometimes also estimated; May et al. 1995, Baillie et al. 2004b). Both methods present limitations, since overall extinction records are, and always will be, incomplete; and species-area relationship have been proved to overestimate extinctions (He & Hubbell 2011). Despite these limitations (Briggs 2014), numerous studies have concluded that the decline of species is occurring at an anomalous rate and has become a global phenomenon.

The generalized process of biodiversity loss and decline has a clear cause: *Homo sapiens* and its activity as part of society, mainly by means of agricultural expansion, logging, overexploitation, and invasive species (Hoffmann et al. 2010a).

Despite the fact that human impacts have been acknowledged long ago (Redman 1999), little improvements have been made to mitigate these impacts. Instead, net global surface of croplands is forecasted to keep increasing in the forthcoming years (Tilman et al. 2001) and demand for wood products is likely to grow (ITTO 2016), in many cases at the expense of natural systems (Gibbs et al. 2010). Unregulated hunting ('bushmeat') and overexploitation have become chronic issues (Milner-Gulland et al. 2003). Invasions are increasingly favored by the current hyper-connected and globalized world, reducing diversity of native ecosystems, introducing diseases or even punctually eliminating native species (Cheng et al. 2011; Vilà et al. 2011; Caves et al. 2013; Simberloff et al. 2013). The magnitude and scope of all these changes is such that a new geological epoch has been defined: the Anthropocene (Steffen et al. 2007)

Vulnerability as a proxy of decline

Knowing how many species have already been lost may serve to warn about the magnitude of the biodiversity loss problem, however, extinction is an irreversible process which allows limited actions once it occurs. Instead, the evaluation of the likelihood of extinction of living species allows for potentially reversing their fates and learning about the circumstances that led them to their current situation. Worldwide, the most complete and used assessment of vulnerability to extinction is **the IUCN Red List of threatened species** (<http://www.iucnredlist.org>), which provides a quantitative evaluation of a wide range of taxa with the greatest spatial scope achievable by currently available information. Criteria to categorize species are mainly based on population size, geographic range and rate of decline of both (IUCN 2001). Different studies support that, not only biodiversity is decreasing at an extraordinary rate, but most living creatures on Earth have become more vulnerable since the nineties (Carpenter et al. 2008; Butchart et al. 2010; Hoffmann et al. 2010b). Assessment initiatives like the Red List also contribute to support conservation planning strategies and guide for national and regional regulations by revealing which species and spaces are more vulnerable and in need of protection.

The study of vulnerability to extinction can be addressed from two different perspectives: the species and the spatial levels. Comparative studies of extinction risk have focused on identifying differences in **vulnerability at the species** (or taxonomic group) **level**. They basically study which life-history and ecological factors, e.g. body size or gestation length, make certain species more prone to extinction (**intrinsic factors**; Webb et al. 2002, Davidson et al. 2009, González-Suárez and Revilla 2013). They occasionally incorporate **extrinsic factors**, i.e. human activities occurring within species' geographic ranges, normally by general indicators such as human population density or human land encroachment (Cardillo et al. 2008; Fritz et al. 2009; Jetz & Freckleton 2015). Individual species' vulnerability reflects a combination of the intrinsic characteristics of the species and/or the extrinsic human threats to which it is exposed.

At the **spatial level**, vulnerability is evaluated by seeking areas where sensitive species and/or ecosystems co-occur with highly impacting activities (threats) and, therefore, where biodiversity loss is more likely to occur. In addition, there are some characteristics of the environment that may increase the probability of extinction, like living in a small island (Russell et al. 1998). Sensitive species can be defined simply as those classified as threatened by the IUCN(IUCN 2015); but additional criteria such as having a small ranges (Jenkins et al. 2013), being endemic to a particular region (Bonn et al. 2002), being rare –according to different definitions (Grenyer et al. 2006)–, or having the features mentioned in the previous section can also be used. **Threats** can refer to natural circumstances, such as geological events or extreme climatic events; or, more frequently, to those directly derived from human activities, such as logging, agriculture, urbanization, etc.

Global indicators of human pressure

Some attempts have been made to classify **threats** in order to implement a common nomenclature and facilitate the exchange of information across projects and practitioners (Salafsky et al. 2008; Balmford et al. 2009). Theoretically, these definitions are suited for species (or any other ecological entity, e.g. population) as

well as ecosystems; and have been implemented by the IUCN, for example, which includes a list of threats for each species, together with their conservation status and additional information on habitat, geographic range, etc. (Table I.1, IUCN 2015b). *Direct threats* are defined as "the proximate human activities or processes that have caused, are causing or may cause the destruction, degradation and/or impairment of biodiversity targets". Some authors distinguish between the source and the mechanism of threat, which causes a stress on the system and modifies the conservation state of the biodiversity target. This causal chain ultimately starts with a driver, normally a socioeconomic condition that triggers the whole process (Fig. I.1; Salafsky et al. 2008).

Broadly, human land use and anthropogenic-induced climate change are considered as the two main direct threats for species and ecosystems (Millenium Ecosystem Assessment 2005). Climate change has received enormous attention in the last decades (Thomas et al. 2004; Bellard et al. 2012); however, many voices argue that attention given to land use change has been unexplainably lower (Titeux et al. 2016). Land use changes has occurred since the beginning of human societies and their consequences are and will likely continue to be more immediate and profound than climate change (Sala et al. 2000). Human land use is the focal threat considered in the present doctoral thesis. Human pressure from **land use** can be measured in different ways. On the one hand, we can quantify land-use **extent**, the areas or proportions of a territory allocated to diverse human land uses (e.g. urban settlements, croplands, extractive forest, etc.). The substitution of a natural habitat for any human use necessarily means some damage to the local communities, at least by means of habitat loss or deterioration (Foley et al. 2005). Still, the magnitude of the impact will depend on the type of use by which natural lands are substituted, e.g. an urban area would almost completely erase a natural system, whereas an extensive agricultural plot may allow the persistence of part of an ecosystem's structure and function. Additionally, within the same type of land use, different **intensities** exist depending on land management. For example, agricultural lands can range from small-scale agro-ecological systems in which diversity can be partially preserved to intensively irrigated plastic-covered lands where no trace of the autochthonous living creatures is left

(Benito et al. 2009; Perfecto et al. 2010). Similarly, forested areas can fluctuate between a pristine tropical rainforest and an intensively managed forest plantation, with very disparate consequences for biodiversity preservation (Redford 1992; Stephens & Wagner 2007; Brockerhoff et al. 2008).

Table I.1. Extract from the threats' classification scheme suggested by the IUCN (Salafsky et al. 2008) to assign to species (version 3.2; IUCN 2012a). All first-hierarchical-level threats are included (bold). For second- and third-levels only examples are given.

1 Residential and commercial development	**5 Biological resources use**
1.1 Housing and urban areas	5.1 Hunting & trapping terrestrial animals
…	5.1.1 Intentional mortality (human use)
2 Agriculture and aquaculture	…
2.1 Annual and perennial nontimber crops	5.2 Gathering terrestrial plants
2.1.1 Shifting agriculture	5.3 Logging & wood harvesting
2.1.2 Small-holder farming	…
…	**6 Human intrusions & disturbance**
2.2 Wood and pulp plantations	6.1 Recreational activities
…	…
3 Energy production & mining	**7 Natural system modifications**
3.1 Oil & gas driling	7.1 Fire & fire suppression
…	…
4 Transportation & service corridors	**8 Invasive & other problematic species & genes**
4.1 Roads & railroads	**9 Pollution**
4.2 Utility & service lines	**10 Geological events**
…	**11 Climate change & severe weather**
	12 Other options

Indirect drivers or **proxies**, such as population growth/density or socioeconomic-development indicators, have also been widely used in studies relating human pressures and biodiversity loss. They represent the underlying common drivers of major proximate pressures, which may be very variable among regions. Socioeconomic changes are the motor of land-use transformation and, more importantly, of policies. Therefore, the understanding of the relationships between socioeconomic development and biodiversity conservation is relevant to advance in decision-making. Although it might be desirable to understand these correlates at the sub-national scale (e.g. County or equivalent administrative units) to be directly transferred into legislation, the reality is that global data are normally available at the country scale (if available at all), which in turn is the common grain size employed to measure international objectives of sustainable development, CO_2 emissions, and

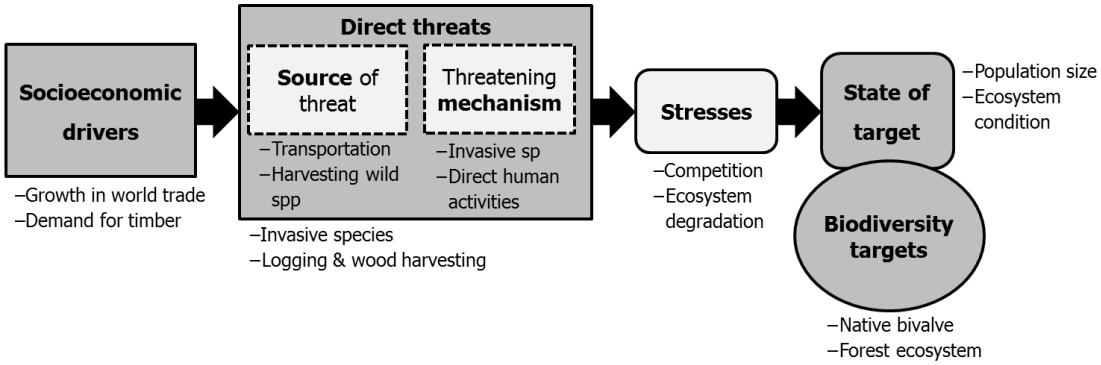


Figure I.1. Elements of the causal chain of threat (adapted from Salafsky et al. 2008, 2009; Balmford et al. 2009). Concepts are inside boxes, examples of each of them are given below. Dark grey boxes represent elements of this chain that are directly addressed in the present doctoral thesis.

other environmental and economic targets (Balmford et al. 2005a; Siche et al. 2008). Another extensively employed indirect driver of human impact is population density or growth, which may be a direct cause of biodiversity decline at fine scales, but which serves more as a proxy of diverse human activities at wider spatial scales (Cincotta et al. 2000; McKinney 2001; Luck 2007). Alternatively, **composite indexes** such as the human footprint are becoming very popular (Sanderson et al. 2002; Ellis & Ramankutty 2008; Alkemade et al. 2009; Geldmann et al. 2014). They present the great advantage of combining information from several sources of human pressure (e.g. land use, population density, accessibility, etc.), but the disadvantage of distancing managers, local people and society as a whole from the ultimate actions that produce damages on natural systems. Both indirect and composite metrics are particularly convenient when working at broad scales, since they capture the general process within larger areas, such as a continent, a biogeographic realm, or the whole Earth.

A final consideration regarding human pressure is the **temporal aspect**. Present activities may impose further damages on natural systems and species, but many of the responses that we see today may be the consequence of past human pressure. Species responses to changes may not be immediate but lagged in time (Tilman et al. 1994; Kuussaari et al. 2009), thus limiting the comprehension of patterns of coincidence between human activities and current biodiversity distribution. In such case, current indicators may not show the whole picture. Studies including past

indicators of human pressure are becoming increasingly common (Dullinger et al. 2013) thanks to the combination of information from different disciplines, such as archeology or paleontology (Boivin et al. 2016), which can be integrated into models to describe past human land use even at the global scale (Kaplan et al. 2011; Ellis et al. 2013). These data are essential because the deplorable conservation status of the whole biosphere is ultimately a consequence of an ensemble of past and present human decisions (Ellis 2015).

The case of terrestrial mammals

Terrestrial mammals have traditionally captured the attention and interest of ecologists and conservation biologists. They are **attractive** species that have been habitually considered umbrella or keystones species (Walpole & Leader-Williams 2002; Roberge & Angelstam 2004). Additionally, they are a relatively **well-known** group of species, with most species identified and their conservation status assessed (IUCN 2015), an available well-resolved phylogeny (Bininda-Emonds et al. 2007), and data are available for multiple ecological and life-history traits (Jones et al. 2009). In addition, they are present on the fossil record, which facilitates inferences based on past evidence (Sommer & Nadachowski 2006; Faurby & Svenning 2015a). Spatial distribution data are also widely available –based on IUCN extent of occurrence maps. Although data may not be very accurate at a fine scale (Rondinini et al. 2006; Smith et al. 2009), at the spatial resolution considered in this thesis (e.g. 1x1º grid cell or country) these distribution data are adequate to minimize omission or commission errors.

To describe mammalian biodiversity much of this thesis uses the **number of threatened mammals**. This biodiversity metric presents the advantage of being a target itself (preserving as many threatened species as possible before they totally disappear) and serving as a diagnostic feature of the conservation status within a certain area (Dobson et al. 1997; Ricketts et al. 2005; Brooks et al. 2006). On the other hand, **terrestrial systems** are probably the most **intensively modified** by humans, after all, our houses, croplands and industrial activities lay on the Earth surface.

Mammals (Fig. I.2), as well as other vertebrates, are primarily threatened by agriculture (Salafsky et al. 2008; González-Suárez et al. 2013; IUCN 2014; Böhm et al. 2016), thus studying this group is relevant and timely to understand the global conservation crisis.

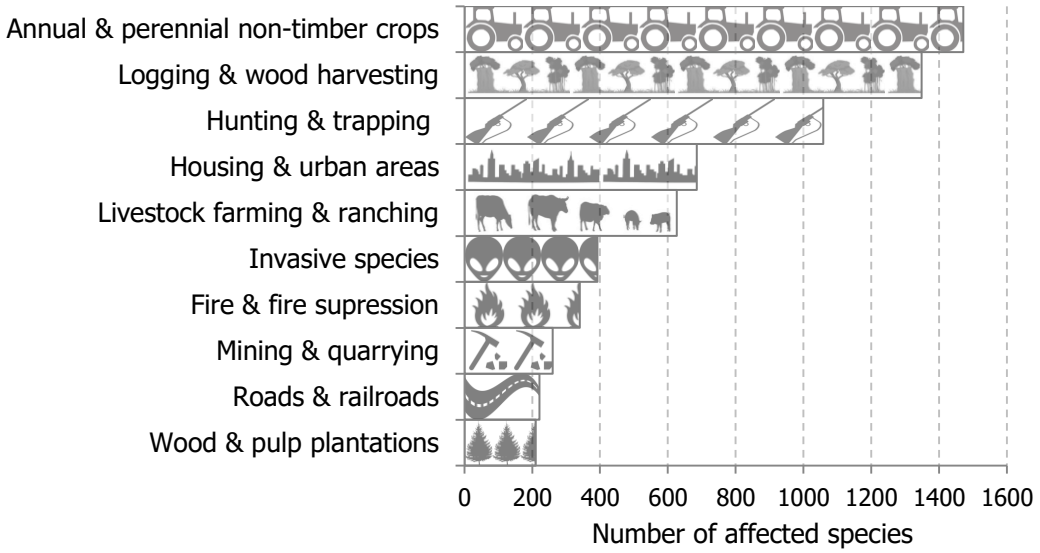


Figure I.2. Most frequent threats listed for terrestrial mammal species, according to the IUCN (IUCN 2013). They correspond to level 1 of the hierarchy classification.

Objectives

In the present PhD thesis spatial vulnerability is investigated, focusing on terrestrial mammal species at a global scale. Species-specific traits, human socioeconomic context and human land use are spatially explored in order to improve our understanding of the differential distribution of threats and threatened species across the world. Specifically, the following questions are addressed:

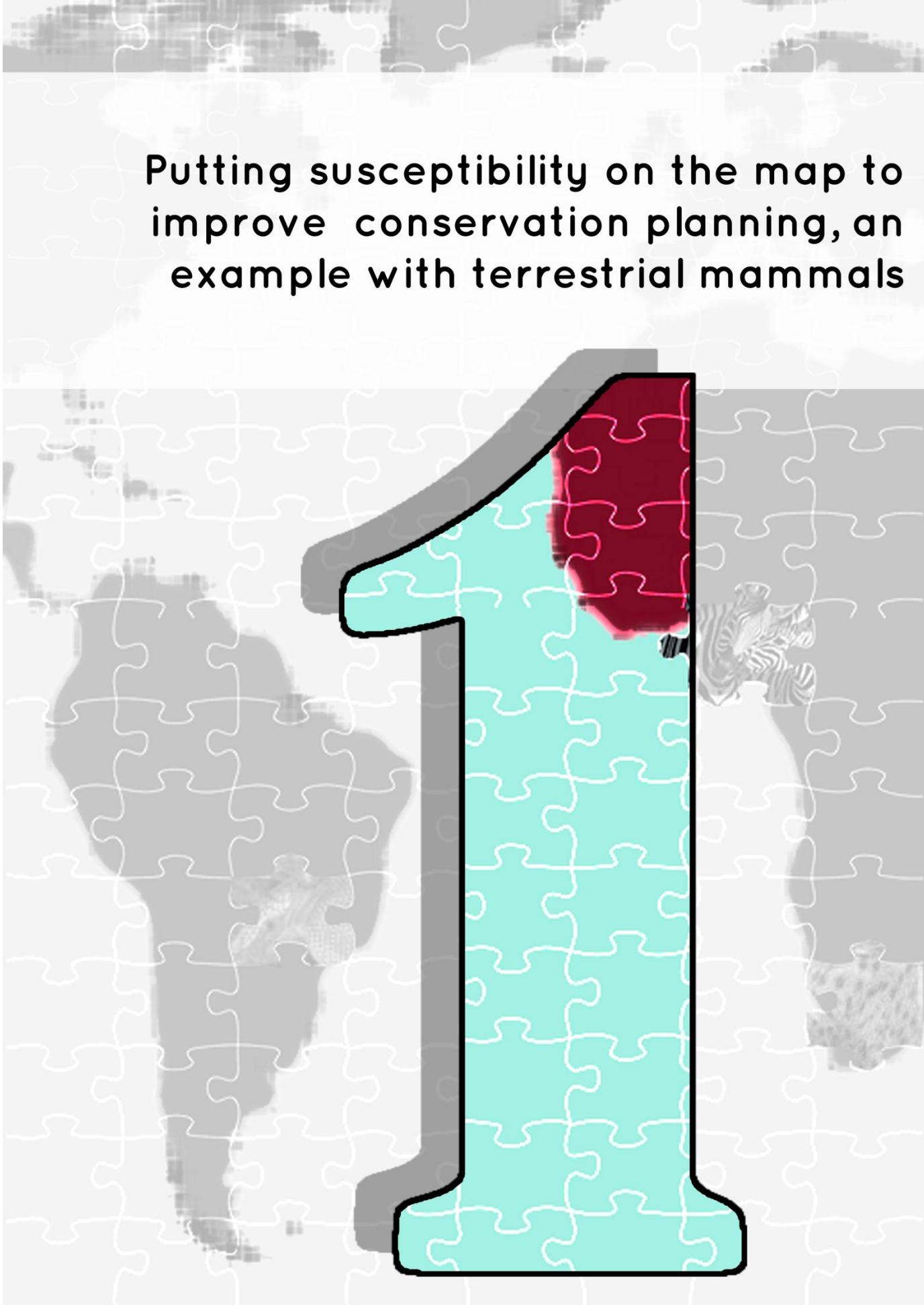
- What is the spatial configuration of the two main sources of vulnerability (intrinsic and extrinsic factors)? Are there regions where one is prevalent, where both coincide, or where neither is relevant? (Chapter 1)

- Which socioeconomic characteristics make a country more susceptible to harbor threatened mammals? (Chapter 2)

- Which facets of human land use: extent, intensity or history, are more informative to explain the distribution of threatened mammalian richness? Are more threatened mammals located in areas where more threatening activities occur or, on the contrary, they predominantly concentrate in relatively low-used areas? (Chapter 3)

- Can past human land-use improve our understanding of species richness distribution? Which metric is most relevant: total area, rates of change, duration of human settlement or remarkable land-use events? (Chapter 4)

Putting susceptibility on the map to improve conservation planning, an example with terrestrial mammals



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Abstract

Here we propose a general approach to spatially synthesize known predictors of vulnerability at the species level in order to identify areas directly associated with specific conservation problems. Under this problem-detection framework, the coincidence or divergence of main strengths and weaknesses can be used to propose tailor-made conservation strategies. This approach is illustrated for terrestrial mammal species at the global scale. We determine, at the species level, the relationships between extinction risk and two well-known predictors of vulnerability: life-history traits (intrinsic) and land use (extrinsic). Transferring these findings into the spatial domain, we identify the areas of the world where one of these two facets is predominant and those areas where both coincide. We recognize four types of area: 1) *double-susceptibility areas*: where both the characteristics of the species and the existing human activities pose a threat, therefore the simultaneous management of both species/habitats and human activities are needed; 2) *intrinsic-susceptibility areas*: where species are naturally fragile and human presence is scarce, thus species-specific management plans would be particularly efficient; 3) *extrinsic-susceptibility areas*: where human pressure is high but species are not intrinsically vulnerable; which requires special attention to human activities; and 4) *low-susceptibility areas*: where there are not remarkable threats for existing terrestrial mammals, which additionally are not particularly fragile. Our approach spatially synthesizes different factors that predispose species to become extinct. This method builds on conservation planning approaches by targeting actions based on known strengths and weaknesses of a given area, and offering a new implementation of comparative studies of extinction risk. This approach may be applied to different species and to particular regions, focusing on different drivers, and complemented by incorporating social and economic trade-offs.

Resumen

A continuación proponemos una aproximación para sintetizar espacialmente conocidos predictores de vulnerabilidad a nivel de especie con el fin de identificar áreas directamente asociadas a problemas de conservación específicos. Bajo este marco basado en la detección de problemas, la coincidencia o divergencia de distintas fortalezas y debilidades se puede usar para proponer estrategias de conservación personalizadas en función de las mismas. Para ilustrar dicha metodología, utilizamos mamíferos terrestres a escala global. Primero determinamos, a nivel de especie, la relación que existe entre el riesgo de extinción y dos grupos de predictores de vulnerabilidad bien conocidos: rasgos de historia de vida (intrínsecos) y usos del suelo (extrínsecos). Transfiriendo estos hallazgos al ámbito espacial, identificamos áreas del mundo donde una de las dos facetas predomina frente a la otra, y áreas donde ambas coincides. En base a ello, es posible reconocer cuatro tipos de área: 1) *áreas de doble susceptibilidad:* donde tanto las características de las especies como las actividades humanas existentes suponen una amenaza, por lo que una gestión simultánea de especies/hábitats y actividades humanas es necesaria; *2) áreas de susceptibilidad intrínseca:* donde las especies son naturalmente frágiles y la presencia humana escasa, planes específicos de gestión de especies serían particularmente eficientes; *3) áreas de susceptibilidad extrínseca:* donde la presión humana es alta pero las especies no son intrínsecamente vulnerables, lo cual requiere fijar la atención en las actividades humanas; y *4) áreas de susceptibilidad baja:* donde no existen amenazas destacables para los mamíferos terrestres, los cuales además no son especialmente frágiles. Así, nuestro método sintetiza los factores que predisponen a las especies a ser más proclives a la extinción. Este método contribuye a la planificación para la conservación, dirigiendo acciones en base a las fortalezas y debilidades de una zona determinada, y ofreciendo una nueva manera de implementar los resultados de los estudios comparativos de riesgo de extinción. La presente aproximación puede utilizarse para diferentes grupos de especies y regiones más acotadas, centrándose en diferentes factores de amenaza, incluyendo factores socioeconómicos.

Introduction

Since Myers (1989, 1990) first identified the now-famous global hotspots of biodiversity, many different criteria have been applied to identify areas of the planet that most "deserve" limited conservation resources (e.g. Olson & Dinerstein 2002) and numerous methods are available to define optimal networks of protected areas (Moilanen et al. 2009). While the practical applications of global prioritization studies have been debated (Tulloch et al. 2015), it is accepted that these efforts are important to raise awareness about where the critical areas and species to preserve are. Indeed, these studies can have great success in mobilizing resources; e.g., by 2003 over US$750 million in funding had been invested in the global hotspots identified by Myers (Brooks et al. 2006).

Systematic conservation planning (SCP) focuses on the spatial facet of conservation actions by identifying important areas for biodiversity that may be considered for protection (Watson et al. 2011), aiming to optimize the benefits per investment of proposed conservation measures and to achieve economically feasible targets (Naidoo et al. 2006; Underwood et al. 2008). SCP largely relies on the concepts of irreplaceability (likelihood that a site is strictly necessary to meet some targets, e.g., preserve the maximum functional diversity) and vulnerability (risk of a site being transformed, e.g., by human use of land), considering that high values of both are desirable to prioritize an area (Margules & Pressey 2000); however, additional properties can be defined to select areas to preserve (see Kukkala & Moilanen 2013 for a review). Furthermore, some studies have incorporated species' intrinsic traits to identify areas to prioritize, e.g., sites where more species are likely to become threatened (Cardillo et al. 2006), or where species recovery would be more probable (Di Marco et al. 2012), demonstrating the value of including knowledge at the species' level into conservation planning.

Nevertheless, conservation-prioritization schemes are supposed to prescribe more than areas to protect (Game et al. 2013). There is a broad spectrum of proposals to complement this approach, such as land use zoning, which proposes a range of management actions for the whole territory (Watts et al. 2009); prioritizing

management of specific threats according to local sensibilities (Carwardine et al. 2012; Auerbach et al. 2015); dynamic reserves' delimitation, accounting for dynamic features of the landscape (Leroux et al. 2007); or specific plans for most endangered species (Vargas et al. 2008), among others. In fact, most of the world land is not a protected area (IUCN & UNEP-WCMC 2015), but other conservation actions can, to a greater or lesser extent, be implemented independently of the protection level of an area; thus there is a need to create guidelines to identify what can and should be done in different regions. Complementing SCP with a global framework to prioritize conservation actions should provide the next step in the identification of valuable areas for conservation while offering practical information relevant for conservation management.

At the species level, the comparative literature on extinction risk has dedicated considerable effort to identify key factors that make some species more vulnerable to extinction. Some of these studies have concentrated on intrinsic species traits (Davidson et al. 2009; González-Suárez & Revilla 2013), others have focused on external drivers related to the degree of anthropization within species geographic range (Pekin & Pijanowski 2012), and some have combined both aspects to compare the importance of intrinsic vs. extrinsic predictors of vulnerability (Cardillo et al. 2005), or to explore their interactions (González-Suárez et al. 2013). Vulnerability reflects a combination of the intrinsic characteristics of the species and the extrinsic human threats to which it is exposed. Incorporating this knowledge into to the spatial facet may help to prioritize actions according to the particular weaknesses and strengths of different areas.

One step forward in the delimitation of areas for conservation is to consider the processes leading to vulnerability in order to develop more targeted conservation actions. In this study we incorporate information on the main predictors of vulnerability at the species level —both intrinsic and extrinsic— and then map areas where they differentially occur, aiming to prioritize conservation actions according to the main weaknesses and strengths of each area. To illustrate our approach, we use global data on terrestrial mammals because this is a charismatic, well-studied group for which data are available at the global scale.

Particularly, we identify intrinsically vulnerable hotspots using data on species' traits that have consistently been associated with vulnerability to extinction at the species level. Additionally, we define extrinsically vulnerable areas as those with higher levels of anthropization, reflecting primarily human land use as a key global threat for mammals. Overall vulnerability is then evaluated combining both types of factors to obtain a global zonation that differentiates susceptibilities and thus, allows distinguishing areas in which different conservation management strategies (e.g., manage the species, manage human activities, or both) may be advisable. The present study does not aim to be a comprehensive review of all known vulnerability factors for particular species or to propose a final global prioritization map for mammals. Instead, we propose and illustrate the potential of an easy-to-implement approach to detect areas of susceptibility and frame conservation actions. Although we use terrestrial mammals as an example here, focusing on few key predictors at a global scale, this approach could be extended to other taxa, other spatial scales, and to include different or additional predictors of vulnerability, with the only constraint of data availability.

Methods

To define spatially-explicit intrinsic and extrinsic vulnerability maps we followed two steps briefly summarized here and described in more detail in the next sections. First, we fitted regression models at the species level (*species-based models*) to define relationships between predictors of intrinsic or extrinsic vulnerability (PV) and global threat status (Fig.1.1A-B). Species' threat status was defined using the IUCN Red List (IUCN 2014) with categories converted into an ordered numeric scale (LC, 0; NT, 1; VU, 2; EN, 3; CR, 4). Second, we used the obtained regression's coefficients to spatially predict vulnerability (*spatial predictions*) according to the characteristics of the terrestrial mammals occurring within each 1ºx1º cell of a grid covering the world's land surface (intrinsic vulnerability), and according to the human land use within each cell (extrinsic vulnerability. Fig.1.1C-D). Finally, we spatially quantified the degree of agreement/disagreement of both vulnerability predictions by means of bivariate local spatial autocorrelation (Fig.1.1E; see below). All spatial data were convened using the

equal-area projection Eckert IV, WGS84, in ArcView 3.2 and ArcGIS 9.3 (ESRI 1999, 2008).

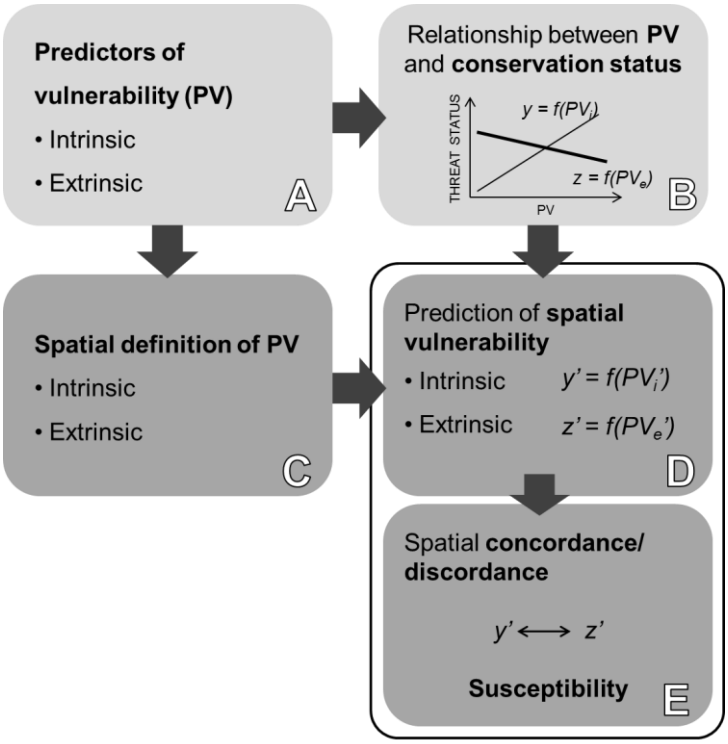

Figure 1.1. Summary of the proposed methodology to prioritize conservation actions. Light grey boxes indicate steps to be taken at the species level; dark grey boxes show steps at the spatial level.

Species-based models: Intrinsic predictors of vulnerability

The selection of traits included in the analyses was based on results from previous studies of extinction risk in terrestrial mammal species at the global scale. A recent publication (Verde Arregoitia 2016) exhaustively reviews this issue. Excluding studies focusing on particular mammalian groups or regions (which have a different scope than the present study) we identified 11 global studies —from the 68 in the review— covering terrestrial mammals in general (see Table 1.S1 in Supplementary Information). Those 11 studies consistently tested and identified as relevant four traits: adult body mass, geographical range, population density and weaning age (Fig. 1.S1). These four traits were also consistently identified as most relevant in the general

review, considering regional- and taxa- specific studies, completed by Verde Arregoitia (2016).

For our analyses we retrieved species-level data for adult body mass, population density and weaning age from the freely available PanTHERIA database (Jones et al. 2009; Table 1.S2). Estimates of the geographic range area for each species were calculated using the IUCN distribution data (IUCN 2014) for terrestrial mammals, selecting only areas identified as native in origin and presence classified as extant or probably extant. We acknowledge that current geographic range is not a purely intrinsic characteristic of a species, since it is widely influenced by external factors, such as climate or human activities (Laliberte & Ripple 2004; Di Marco & Santini 2015). Still, geographic range sizes capture ecological and dispersal attributes that can influence extinction risk and are not well-captured by any of the other intrinsic or extrinsic vulnerability indicators included in the present work.

We accounted for lack of independence when working at the species level by adjusting phylogenetic generalized least-squares (PGLS) regressions based on the updated mammalian supertree of Bininda-Emonds et al. (2007) presented by Fritz et al. (2009). PGLS models were fitted using the procedure *pgls* within the R-package 'caper' (Orme et al. 2013; R Core Team 2014). Correlation among predictors was tested to avoid collinearity (Table 1.S3). Population density was excluded, due to its high correlation with adult body mass (ρ =-0.76) and its lower sample size. PGLS included the selected intrinsic traits as independent variables ($\log_{10}$-transformed) and the numeric IUCN threat status as the dependent variable. This simplification considers IUCN categories as a continuous and thus, assumes differences among categories are equal, which may not be realistic. Nevertheless, using a numeric threat status allows us to account for phylogenetic signal in explanatory variables, to rank predictions from lower to higher risk, and to easily compare our findings with previous literature using equivalent approaches (e.g. Purvis et al., 2000; Di Marco et al., 2012). Species with status defined as Data Deficient (DD), Extinct (EX) or Extinct in the Wild (EW) were not considered for the analysis (N_{DD}=788; N_{EX}=73; N_{EW}=2). To avoid circularity we excluded species listed as threatened by the IUCN under criteria B (based on the size of their geographic range, N=554). In addition, some species could not be included

because phylogenetic relationships were not defined (N=13) or trait data were not available for all three traits (N=2953). The final model was fitted for 981 terrestrial mammal species.

Acknowledging the reduced and biased sample size representing intrinsic vulnerability of terrestrial mammals, we fitted alternative models to assess sensibility of results to data availability. To increment the sample size, we (1) included all terrestrial mammals not excluding species listed under criterion B but eliminating geographic range as a predictor (sample size increased to N=1027); and (2) built a model including the two most data-complete and least correlated traits: body mass and geographic range (Table 1.S3; sample size increased to N=2747). (3) We considered the option of imputing missing data as done in recent studies based on large incomplete trait databases (Di Marco & Santini 2015), acknowledging that they are likely missing not at random (Nakagawa & Freckleton 2008). To do that, we employed the *phylopars* and *phylopars.predicts* functions from the 'Rphylopars' package in R (Goolsby et al. 2015); this approach incorporates phylogenetic information and relationships among variables to impute data and has been shown to perform well imputing data for similar traits (Penone et al. 2014). However, for weaning age we lack data for >70% of species, thus, results based on imputed data need to be interpreted with caution. Lastly, to explore the biases in data availability between small and large species (because the latter are better studied; González-Suárez et al. 2012) we performed separate analyses for small (body mass ≤3kg; Cardillo et al. 2005) and large mammals (body mass> 3kg).

Species-based models: Anthropogenic predictors of vulnerability

We estimated the degree of anthropization within each species geographic range based on the anthromes global classification by Ellis & Ramankutty (2008). In particular, we used the series corresponding to the year 2000 from "Anthropogenic Biomes v.2" (Ellis et al. 2010). This classification provides an integrated perspective with a gradient ranging from low to highly modified areas, and recognizes six broad groups (anthromes): wildlands (woodlands and barren lands), semi-natural lands

(inhabited woodlands and barren lands), rangelands, croplands, villages and dense settlements (Table 1.S4).

As in the previous section, we fitted PGLS to test the relationship between anthromes' composition at the species level and IUCN threat status as a numerical response. The predictors were the proportions of each species' range covered by each of the anthromes mentioned above. Due to topological errors (discrepancies between IUCN geographic ranges and anthromes spatial database), for some species the sum of all anthromes proportions represented <95% of their geographic range; these species were not included in the analyses (N=86, Table 1.S5). Species not included in the phylogeny were also excluded (N=440). Compositional data present challenges for analyses because of the implicit relationship between proportions: the increase of one necessarily implies a decrease in another (or several at the same time), which is not reflected by a simple correlation test (Table 1.S6). As in Aitchison & Egozcue (2005) we used a log-ratio transformation: one category is defined as a reference (in our case dense settlements, the most modified anthrome) and the other values are calculated as ratios from that reference. We used the Aitchison zero replacement procedure (Aitchison 1986) as described in Fry et al. (2000), which replaces values as follows:

$$C_i = \begin{cases} \delta(M+1)(N-M)/N^2 & component = 0 \\ i - (\delta M(M+1)/N^2) & otherwise \end{cases} \quad \text{Eq 1.}$$

Where, C_i is the new component value (in parts per unit), δ is the maximum rounding error (we used the minimum overlapping percentage estimated: $8.02 \cdot 10^{-7}$), N is the total number of components (in our case always 6), M the number of components that are zero (which varies among observations), and i is the original component with a non-zero value.

Because distribution data were available for many more species than life-history trait data, the number of species available for this analysis was notably higher than in the traits-based models. To ensure that differences in sample size were not driving our results, we defined anthropogenic models for both the whole set of species with distributional data meeting the requirements above (N=3908), and the same

subset of species for which the main intrinsic-traits model was fitted. To partly account for the fact that different species may be exposed to different threats (González-Suárez et al. 2013), and to allow for the assessment of spatial coincidence/divergence in relation to intrinsic vulnerability, we also built separate models for small (body mass ≤3kg. $\delta = 8.02 \cdot 10^{-7}$ in eq. 1) and large terrestrial mammals (body mass> 3kg. $\delta = 1.99 \cdot 10^{-6}$ in eq. 1). Additionally, we built a full model including both intrinsic and extrinsic predictors to weight the relative contribution of each of them in explaining threat status (Table 1.S7).

Spatial predictions

To make spatial predictions from the species-based models we first defined a 1x1º grid covering the world emerged surface. We overlapped this grid with the IUCN geographic distribution range data for each mammalian species to determine which species occur in each cell. To predict intrinsic vulnerability per grid cell, we defined cell values of body mass, geographic range and weaning age as the median value obtained from all species occurring in a given cell and for which trait data were available. These median trait values aim to depict the representative mammal occurring within each grid cell. Medians were preferred over mean values to counteract the overrepresentation of large mammals in the life-history traits database. For predicting extrinsic vulnerability we superimposed the 1x1º global grid and the anthromes layers to calculate the proportion of each cell occupied by each of the anthrome categories. Proportion values (compositional data) were transformed using equation 1 ($\delta = 1.28 \cdot 10^{-06}$). Alternatively, we predicted intrinsic and extrinsic vulnerability (separately) as the mean species-based vulnerability for all present species in each grid cell (Cardillo et al. 2006).

Finally, to evaluate the spatial coincidence of both types of vulnerability, we computed bivariate local Moran's I values (local indicators of spatial association, LISA) and cluster maps with the software GeoDa (Anselin et al. 2006), considering first order queen spatial weights (cells sharing at least one point are neighbours), and a significance level of $p < 0.01$ for cluster inclusion. This analysis classifies clusters based on the values of each grid cell and its neighbouring grid cells; four combinations are

possible high-high, low-low (both positive spatial autocorrelation values), high-low and low-high (both negative spatial autocorrelation values). High or low values are defined in relation to the mean value of the given set of data; i.e. high values of intrinsic vulnerability are those over the mean predicted intrinsic vulnerability for all grid cells, and low values are those under the mean; and the same for extrinsic vulnerability.

Results

Species-based models: Intrinsic predictors of vulnerability

As expected, our regression analyses suggest that larger mammals, occupying small geographic ranges and with older weaning age tend to be at higher risk (Table 1.1). These relationships are generally supported by alternative versions of the model (Table 1.S8), except for the alternative model including imputed data which suggests that earlier weaning ages increase risk, a biologically counterintuitive result (Model I4, Table 1.S8). This relationship appears to be an artefact of the imputation technique itself, as imputed data values vary widely depending on the different subset of variables that are considered for the imputation (Fig. 1.S2). Results based on data imputation for traits with significant data gaps needs to be interpreted with great caution and here we feel relying on non-imputed data is more sensible. The model including three traits (without imputation) presents the highest adjusted R^2, similarly to the alternative model excluding weaning age, with practically identical coefficient estimates (Model I3, Table 1.S8). Broadly, results are qualitatively the same when large and small mammals are analyzed separately, except that weaning age is not a significant predictor of threat status for large mammals (Table 1.1).

Species-based models: Anthropogenic predictors of vulnerability

Our analyses suggest that greater overlap with croplands and semi-natural lands is associated with higher threat status in terrestrial mammals; whereas greater overlap with wildlands is associated with lower risk (for all mammals, and for large and

Table 1.1. Results of the species-based phylogenetic generalized least squares (PGLS) models testing the association of four intrinsic traits with threat status in terrestrial mammals. Models excluded species classified as threatened following criterion B and with information for the four traits. Models were fitted for all terrestrial mammals (*All*), small terrestrial mammals (body size≤3 kg. *Small*), and large terrestrial mammals (body size>3 kg. *Large*). Traits were $\log_{10}$-transformed prior to analyses. We report regression coefficient estimates (β) with their standard errors (*SE*), as well as the number the species analyzed in each model (N).

Traits	**β (SE)**		
	All (N=981)	*Small* (N=678)	Large (N=303)
Geographic range	-0.45 (0.028)***	-0.31 (0.024)***	-0.76 (0.068)***
Weaning age	0.26 (0.127)*	0.24 (0.103)*	-0.02 (0.284)
Body mass	0.29 (0.047)***	0.10 (0.038)**	0.55 (0.151)***
Adjusted R^2	0.25	0.23	0.32

*** p<0.001; ** p<0.01; * p<0.05; ·p<0.1

Table 1.2. Results of the species-based phylogenetic generalized least squares models (PGLS) testing the association between the distribution range *anthromes'* composition and threat status in terrestrial mammals. *Anthromes* represent log-transformed ratios between each category and the "dense settlements" category (more detail in the methods). Models were fitted for all terrestrial mammals (*All*), small terrestrial mammals (body size≤3 kg. *Small*), and large terrestrial mammals (body size>3 kg. *Large*). We report regression coefficient estimates (β) with their standard errors (*SE*), and the number the species analyzed in each model (N).

Anthromes	**β (SE)**		
	All (N=3908)	*Small* (N=2404)	*Large* (N=508)
Villages	0.00 (0.010)	0.01 (0.011)	0.05 (0.045)
Croplands	0.08 (0.012)***	0.05 (0.014)***	0.10 (0.049)·
Rangelands	0.00 (0.009)	0.10 (0.011)***	-0.10 (0.030)**
Semi-natural lands	0.22 (0.012)***	0.12 (0.015)***	0.54 (0.051)***
Wildlands	-0.17 (0.009)***	-0.18 (0.012)***	-0.24 (0.034)***
Adjusted R^2	0.13	0.11	0.24

*** p<0.001; ** p<0.01; * p<0.05; ·p<0.1

small species separately). Overlap with villages has no significant effect in any of the tested models (Tables 1.2 and 1.S9). Greater overlap with rangelands has no significant effect when all mammals are analyzed together likely because there are opposite effects between groups: more overlap is associated with higher risk in small mammals but with lower risk in large mammals (Table 1.2). Results are qualitatively the same for

a model fitted only for species with available intrinsic traits' data, with a notable decrease in the adjusted R^2 (Table 1.S9).

Overall, species-based models based on intrinsic traits have more explanatory power than those based on anthropogenic effects, with more pronounced differences when comparing models fitted for the same subset of species (Model I1 vs. A2, Tables 1.S8 and 1.S9). However, anthropogenic variables clearly play a role in explaining species' threat status (Tables 1.1 and 1.2) as supported when both intrinsic and extrinsic indicators are analyzed together (Table 1.S10).

Spatial predictions

Here we focus on predictions based on median trait values per grid cell (intrinsic vulnerability) and extrinsic vulnerability predicted from the proportion of grid-cell covered by different anthromes (extrinsic vulnerability). These predictions are the most robust to data biases and limitations (i.e., which subset of mammals is employed to fit the species-based models; Appendix 1.S3). Broad scale differences between this approach and the alternative approach of averaging the predicted vulnerability for all species occurring within a grid-cell are generally small, being more evident for extrinsic vulnerability, where predictions are correlated only at 0.60 (Spearman's ρ; Table 1.S12, Fig. 1.S4). Comparing intrinsic vulnerability predictions, they present Spearman's ρ correlation values between 0.77 (full model) and 0.91 (including only geographic range and body mass, and imputing data; Table 1.S11, Fig. 1.S3). Further discussion of these different outputs is included in Appendix 1.S3.

Vulnerability due to intrinsic predictors is estimated for a total of 17980 grid cells, which represent approximately 134.2 M km^2 of emerged land (99.4% of the total World's land area, excluding Antarctica). Considering all mammals and based on median trait values per grid cell, we find that high intrinsic vulnerability areas occur in diverse parts of the world, including Southeast Asia, India, southern and Horn of Africa and the Andes. Areas of low intrinsic vulnerability include most of South America, and Europe (Fig. 1.2A).

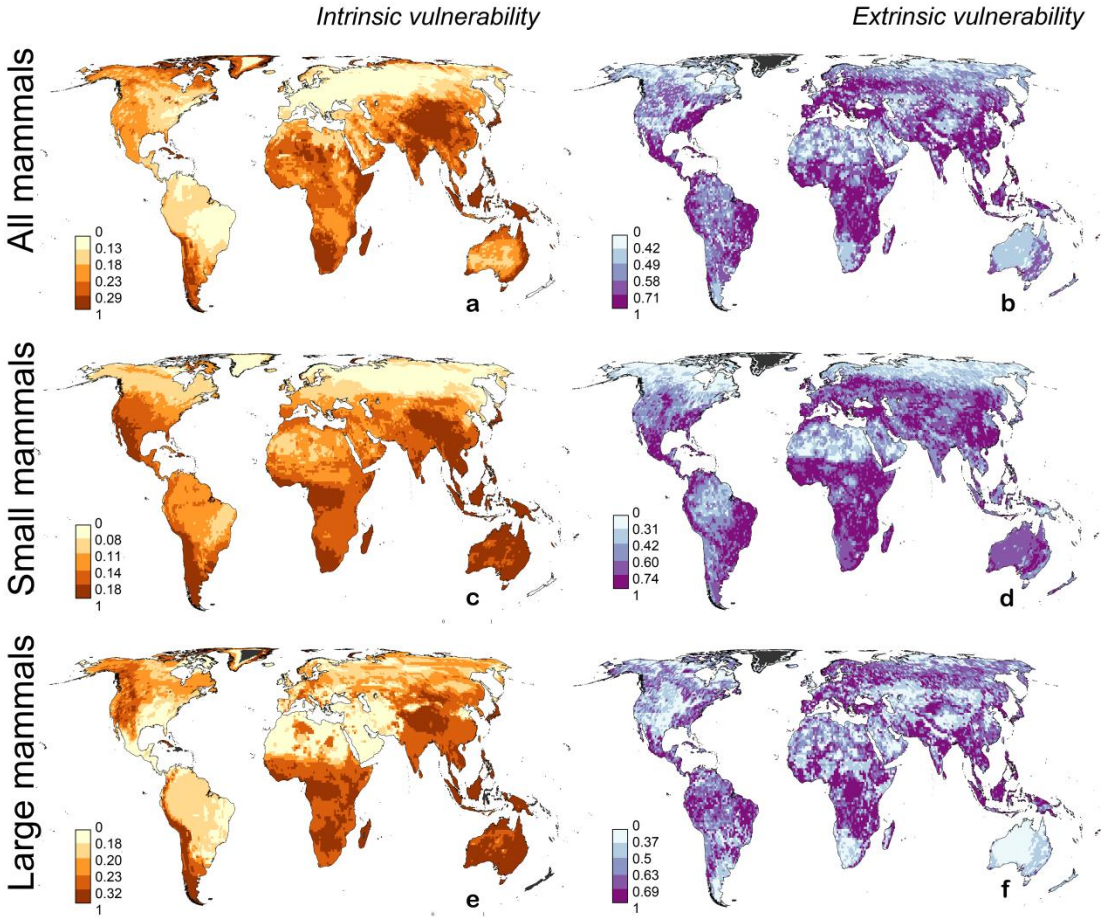

Figure 1.2. Predicted intrinsic (*a*) and extrinsic (*b*) vulnerability based on all terrestrial mammal species, and separately for small (body size≤3kg; *c* & *d*) and large species (>3kg; *e* & *f*). All predictions (of continuous Red List Status) are standardized between 0-1 to facilitate comparison. Legend categories are based on quantiles. More intense colors indicate higher vulnerability. Black areas indicate no data.

Separate predictions for large and small mammals reveal interesting differences. For example, vulnerability in northern Africa is mostly associated to smaller species (Fig. 1.2c). In addition, new areas of high intrinsic vulnerability are revealed when examining only small mammals, including Central and South America, and southern Europe (Fig. 1.2c). Additional patches are revealed in northern Europe and Russia when considering only large mammals (Fig. 1.2e). Overall, vulnerability patterns are not preeminently driven by any of the two subgroups, with low values of correlation between all-large (Spearman's ρ=0.19), and all-small (ρ=0.20) predictions.

Vulnerability due to extrinsic predictors is estimated for 17631 grid cells, covering around 133.7M km² (98.9% of the World's emerged land, excluding Antarctica). The included surface is slightly smaller than in the intrinsic analysis because Greenland is not included in the anthromes classification. High extrinsic vulnerability areas occur in numerous areas of the World, reflecting widespread human impacts, and include eastern United States, Central America, the coast of Brazil, most of Sub-Saharan Africa, Europe and South East Asia, China, Pakistan, and India (Fig.1.2b). Predictions based on the separate models for small and large mammals show similar, highly correlated patterns (all vs. small ρ=0.81, all vs. large mammals ρ=0.84. Figs.1.2d and 1.2f).

Estimates of spatial association of both vulnerabilities —based on bivariate local Moran's I values— was possible for 17474 grid cells based on the ensemble of terrestrial mammals with available information. We identify four types of clusters: *double-susceptibility* areas (~20.1M km²), where high values of intrinsic vulnerability are surrounded by high values, or vice versa (significant positive spatial autocorrelation; $p<0.01$); *intrinsic-susceptibility* areas (~ 12.3M km²), where high intrinsic vulnerability values are surrounded by low extrinsic values, or low extrinsic values are surrounded by high values of intrinsic vulnerability (significant negative spatial autocorrelation); *extrinsic-susceptibility* areas (~25.5M km²), where high values of extrinsic vulnerability are surrounded by low intrinsic vulnerability, or low intrinsic vulnerability values are surrounded by high values of extrinsic vulnerability (significant negative spatial autocorrelation); and *low-susceptibility* areas (~16.7M km²) where low values of intrinsic vulnerability are surrounded by low extrinsic vulnerability values, or vice versa (significant positive spatial autocorrelation). *Double-susceptibility* areas occur primarily in Southeast Asia, Madagascar and Sub-Saharan Africa. *Intrinsic-susceptibility* areas are primarily located in the Sahara region, Botswana-South Africa, Tibet and near the Arctic in the American continent. *Extrinsic-susceptibility* areas occur in most of Europe, North America, Brazil and parts of southern Africa. *Low-susceptibility* areas are essentially found in Siberia and small regions of Europe, North and South America (Fig. 1.3a). The four types of areas together represent 56% of the global surface for which data are available. The

remaining areas present intermediate values of intrinsic and extrinsic vulnerability which are not assigned to particular clusters. (Additional information about zones is included in Appendix 1.S3).

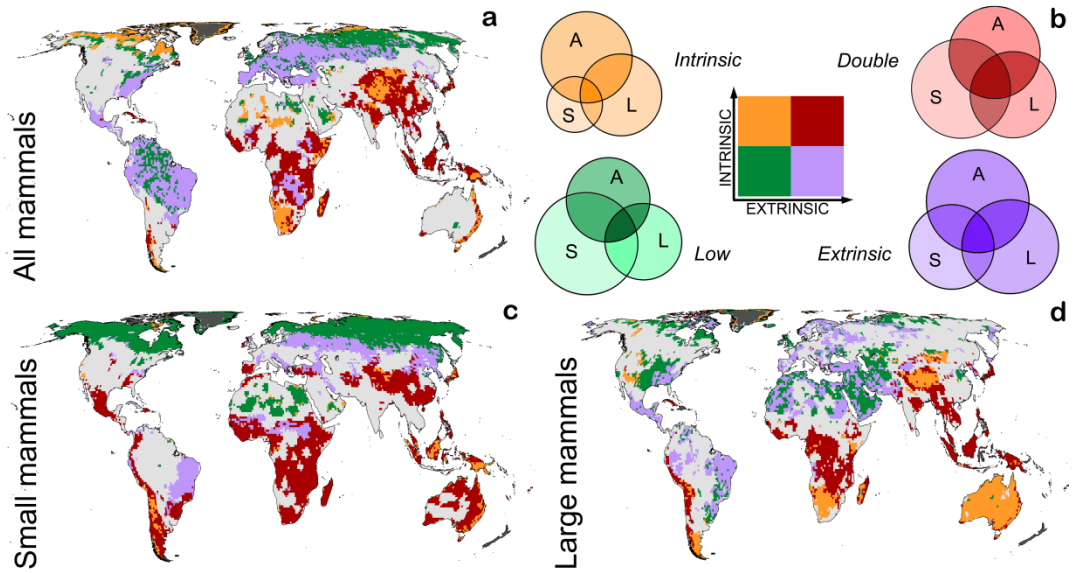

Figure 1.3. Zonation based on the concordance or discordance between intrinsic and extrinsic vulnerability, for all terrestrial mammal species (*a*), and separately considering small (body size ≤3kg; *c*) and large species (>3kg; *d*). The four types of zone (double-, low-, intrinsic- and extrinsic- susceptibility) are delimited by calculating bivariate local Moran's I. Panel *b* shows Venn diagrams (one for each type of zone) of the spatial agreement among predictions based on all mammals (*A*), only small (*S*) and only large species (*L*). The legend in panel *b* applies for both the maps and the diagrams; horizontal axis represents extrinsic vulnerability and vertical axis, intrinsic vulnerability.

Separate cluster analyses for small (16948 grid cells) and large terrestrial mammals (17183 grid cells) present largely different pictures (Fig. 1.3). Venn diagrams show how the four zoning categories coincide among the three groups of species (all, small and large; Fig. 1.3b); overall we find relatively low spatial overlap in assigned cluster type. A 38% of grid-cells classified as *double-susceptibility* areas including all species are equally allocated for separate groups of species, 17% in the case of *extrinsic-susceptibility* areas, and 18% of *low-susceptibility* areas, whereas only 7% of *intrinsic-susceptibility* areas are equally assigned for all groups. *Low-susceptibility* or *double-susceptibility* areas are more widespread when only small species are analyzed; and

extrinsic-susceptibility areas occupy the vastest surface when considering large mammals separately (Fig. 1.3).

Discussion

Understanding the processes driving vulnerability patterns (or irreplaceability, or any other property worth preserving) should be as important as ranking areas as priority for conservation. With this understanding we can move from a prioritization framework to a problem-detection approach that could lead to more effective conservation planning and more informed management decisions. Information about the factors that drive vulnerability is increasingly available at the species level (Kleyer et al. 2008; Frimpong & Angermeier 2009; Jones et al. 2009), therefore, the easy-to-follow protocol we present here could be applied to different taxa and at different spatial scales. This approach requires five steps (Fig.1. 1). The first step is to identify relevant predictors of vulnerability (PV) for the selected group of species (Fig. 1.1A; e.g. life-history determinants and land use). The second step requires selecting a measure of conservation status (e.g. IUCN status) and establishing the relationship between status and PV (Fig. 1.1B). The third step is to define the region of interest (e.g. the world emerged surface) and calculate the selected PV values for discrete spatial units (e.g. 1x1º grid cells; Fig 1.1C). In step 4 we spatially predict conservation status at the new selected unit (i.e. grid-cell spatial vulnerability; Fig. 1.1D) based on the identified relationship between PV and conservation status at the species level. The final step consists on evaluating the coincidence or divergence of extreme values of these predictions by any measurement of spatial association (e.g. bivariate local Moran's I) to obtain a spatial summary of the main factors considered and, consequently, to reveal and help prioritize conservation actions within different areas.

The identification of PV does not need to be exhaustive. As illustrated in the present work, the final goal may not be to include all known factors influencing species conservation, but to summarize the ones of interest (e.g., because they are the most worrying in a given area or time) and spatially compare them. Although the two groups of variables considered in the present work are not completely independent

(e.g. geographic range is determined by intrinsic properties of a species, like dispersal ability, as well as extrinsic human factors; Di Marco & Santini, 2015), they represent the two main components of vulnerability discussed in the literature of comparative extinction risk analyses. Certainly, our analysis is a simplification, as other life-history traits (e.g. litter size, diet specialization) and external threats (e.g. invasive species, fire) are relevant for some groups and regions, but generality requires focusing on broad, key factors affecting most species. Moreover, to complement the spatial summary, explicit descriptors of socioeconomic development could be considered in order to better define the human context in which decisions are going to take place (Polaina et al. 2015).

The final proposed zonation categories offer a useful summary, which does not reflect hierarchical priorities but categorical descriptors, i.e. *double-susceptibility* are not more important than the rest, although they may require more resources given their conflictive situation. In fact, the four zone-categories are not a definitive guide for management; additional (or fewer) zones may be defined depending on the conservation goals and available data and resolution. Nevertheless, these categories are useful to identify different types of regions for which diverse management actions may be most useful.

Double-susceptibility areas are, by definition, zones that harbour naturally sensitive fauna, which may be charismatic species able to capture public and institutional attention (Roberge & Angelstam 2004), but also may represent difficult — and expensive— conservation targets (Andelman & Fagan 2000). Human activities in these areas may also play an important role to threaten species. In our global analyses we found that an important portion of these areas is currently classified as seminatural (Fig. 1.S5) and thus, with potential for human land uses to intensify (Neumann et al. 2010). Proposing conservation actions in these areas requires making difficult trade-offs, since human needs are certainly going to confront with the conservation of sensitive species (Dobrovolski et al. 2011).

Intrinsic-susceptibility areas present similar characteristics to *double-susceptibility* areas in terms of sensitive fauna; with the subsequent mentioned advantages and difficulties. Human land use in these areas is less threatening in

general (mainly deserts and remote areas; Fig. 1.S5); thus, human-wildlife conflicts are less likely, which a priori would facilitate any conservation action. Nevertheless, human impact may still exist as threats such as hunting and persecution may be a high risk factor for sensitive fauna, including larger species (González-Suárez & Revilla 2014).

Extrinsic-susceptibility areas are occupied by species with low intrinsic vulnerability, potentially able to cope with the existing high levels of anthropization (e.g. Wilson et al. 2014); therefore, these areas should be easier to manage. Still, any effective conservation strategy within these areas should include close monitoring of species and an important control of human expansion in the form of land-use intensification, because additional anthropogenic activities could compromise the conservation of even widespread and resilient species. Importantly, many of these regions may actually no longer be intrinsically vulnerable because sensitive species went extinct time ago (Morrison et al. 2007). If correctly managed or restored, these areas could potentially host some of these species again.

Low-susceptibility areas have low-intrinsically vulnerable species and low human impacts. These areas are relatively safe because key factors associated with species vulnerability are largely absent or have limited impact. They present an opportunity to implement potentially inexpensive, low-conflict passive conservation actions that may contribute to maintain the low-susceptibility status in the long term (Sanderson et al. 2002). Nevertheless, additional threats, not included in the analyses, may exist in these areas, so specific recommendations would require a careful evaluation of threats and impacts.

Data quality is a recurrent issue in global analyses including many species; however, our results prove that delimitating broad patterns, differences are generally not qualitative, and that high vulnerability areas can be consistently detected (Appendix 1.S3). Nevertheless, there are likely data biases regarding human land use descriptors, including the fast changes that are occurring in some areas (Verburg et al. 2011) or differences in data quality across regions, which we could not explore and that could influence zonation schemes. At the species level, our analyses for terrestrial mammals reveal intrinsic traits as better predictors of the IUCN threat status than the

extrinsic factors considered here (namely land use), in agreement with previous studies (e.g. Cardillo et al. 2004). However, this does not imply that external factors are irrelevant, but instead, that this type of statistical methods may adjust better to life-history traits. Species-based models' explanatory power may seem overall low (Adj.R^2<0.3), however, these low values are in fact higher than the average variance explained by other ecological/evolutionary works (Jennions & Møller 2002).

In this study we also explored different approaches to map the main findings at the species level (namely using a median descriptor of traits, or averaging species predictions), which are congruent at the broad scale, but reveal important regional differences for both intrinsic (e.g. Northern South America is often predicted as a low vulnerability area, but in some cases it is detected as vulnerable; Fig. 1.S3) and extrinsic vulnerability (e.g. North America is a low extrinsic vulnerability area when considering mean predictions, but patches of high vulnerability emerge when using real cover values per grid cell; Fig. 1.S4). These regional discrepancies should not be overlooked if using this approach to define conservation actions and strategies. In our example we also found different zonations when small and large terrestrial mammals were analyzed separately. While this separation had an illustrative purpose (to show the effects of data biases) it is important to notice how patterns vary depending on the particular subset of species. For example, in the case of small species, the vast coverage of *double-susceptibility* areas (Fig. 1.3) suggests that more human-wildlife conflicts may occur for this subgroup of species than detected by the all-species prediction.

A bewildering mix of advice for global conservation planning has been produced in recent years aiming to delimit the minimum area necessary to protect the endangered species/ecosystems of the world; however, we are still witnessing a decrease in global biodiversity (Ceballos et al. 2015). Here, we present an approach to detect spatial differences in risk which also allows extracting the most of valuable information at the level of species, populations and, potentially, other ecological entities. Focusing on patterns and ignoring the, often complex, processes that drive those patterns can lead to simplistic and inefficient biodiversity conservation strategies (Peres & Terborgh 1995).

Acknowledgments

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Supporting Information

Appendix 1.S1. Species-based models: data

Intrinsic predictors of vulnerability

From the eleven consulted articles, seven of them considered exclusively biological/ecological variables describing species' traits (Morrow & Fricke 2004; Davidson et al. 2009; Liow et al. 2009; Verde Arregoitia et al. 2013; González-Suárez & Revilla 2013; Chen 2014; Polishchuk et al. 2015). Three others included species' traits and additionally explored the role of human variables and environmental indicators describing conditions within species geographic range (Cardillo et al. 2005, 2008; Jetz & Freckleton 2015). The last study evaluated environmental and socioeconomic characteristics within ecoregions, predicting risk levels by ecoregion instead of for specific species (Fritz et al. 2009). Studies focusing on a certain subgroup of mammals, or not covering the whole Earth surface were discarded, based on the review in Verde Arregoitia (2015) .

Table 1.S1. Summary of the reference studies (N=11). Variables found to have a significant effect on the response variable (IUCN global threat status, converted to numeric) are in bold.

Reference	Statistic model	Intrinsic variables	Other variables
Cardillo et al. 2005	Multiple regression on phylogenetically independent contrasts	- Age eyes' opening - Age first breeding - Body mass - Diet - Diurnality - **Geographic range** - Gestation length - Habitat mode - Home range - Interbirth interval - Island endemic - Litter size - Litters per year - Neonatal body mass - **Population density** - Population size - Sexual maturity age - Social group size - Terrestriality - Trophic level - **Weaning age**	- 5th percentile of HPD - External threat index - **Human population density (HPD)** - **Latitude**

Reference	Statistic model	Intrinsic variables	Other variables
Cardillo et al. 2008	GLM (with previous phylogenetically independent contrasts)	- Age eyes' opening - Age first breeding - Body mass - Diet - Diurnality - **Geographic range** - Gestation length - Habitat mode - **Home range** - Interbirth interval - Island endemic - Litter size - Litters per year - Neonatal body mass - **Population density** - Population size - Sexual maturity age - Social group size - Terrestriality - Trophic level - **Weaning age**	- **Human population density (HPD)** - 5th percentile of HPD - External threat index - Latitude
Chen 2014	Polyserial correlations	- **Geographic range** - **Areal size of high suitable habitat** - **Areal size of intermediate suitable habitat** - **Areal size of low suitable habitat**	
Davidson et al. 2009	Decission-tree models	- **Body mass** - **Diurnality** - **Geographic range** - **Habitat mode** - **Home range** - Island endemic - **Population density** - **Social group size** - Sociality - **Speed of life history** - Trophic level	
Fritz et al. 2009	Phylogenetic generalized linear model	- **Body mass** - **Geographic range** - Gestation length - **Population density** - **Weaning age**	*(Ecoregional scale)* - Ecoregion area - Habitat heterogeneity - Historic agriculture index - Mean annual actual evapotranspiration - Mean elevation - Mean gross domestic

Reference	Statistic model	Intrinsic variables	Other variables
			product - Mean human appropriation of net primary productivity - Mean human influence index - Mean human population density - Proportion of cropland in 2000 - Proportion of urban land cover in 2000
González-Suárez & Revilla 2013	Taxonomically informed GLMM	- Body mass - **Body mass variability** - **Geographic range** - Litter size - Litter size variability - **Population density** - Population density variability - **Sexual maturity age** - Sexual maturity age variability - Weaning age - Weaning age variability	
Jetz & Freckleton 2015	Phlyogenetic generalized least-squares (PGLS)	- **Body mass** - **Geographical range**	- **Human encroachment**
Liow et al. 2009	Phylogenetic independent contrasts	- **Body mass** - **Geographic range** - **SLOH (sleeping or hide) behavior** - **Trophic level**	
Morrow & Fricke 2004	Comparative analysis of independent contrasts (CAIC)	- Sexual dimorphysm - Testes size	
Polishchuk et al. 2015	Mixed-effects logistic regression model	- **Body mass** - **Nonsynonymus to synonymus sustitutions (Ka / Ks)**	
Verde Arregoitia et al. 2013	Phylogenetic generalized linear mixed model (PGLMM)	- **Body mass** - Net diversification rate	

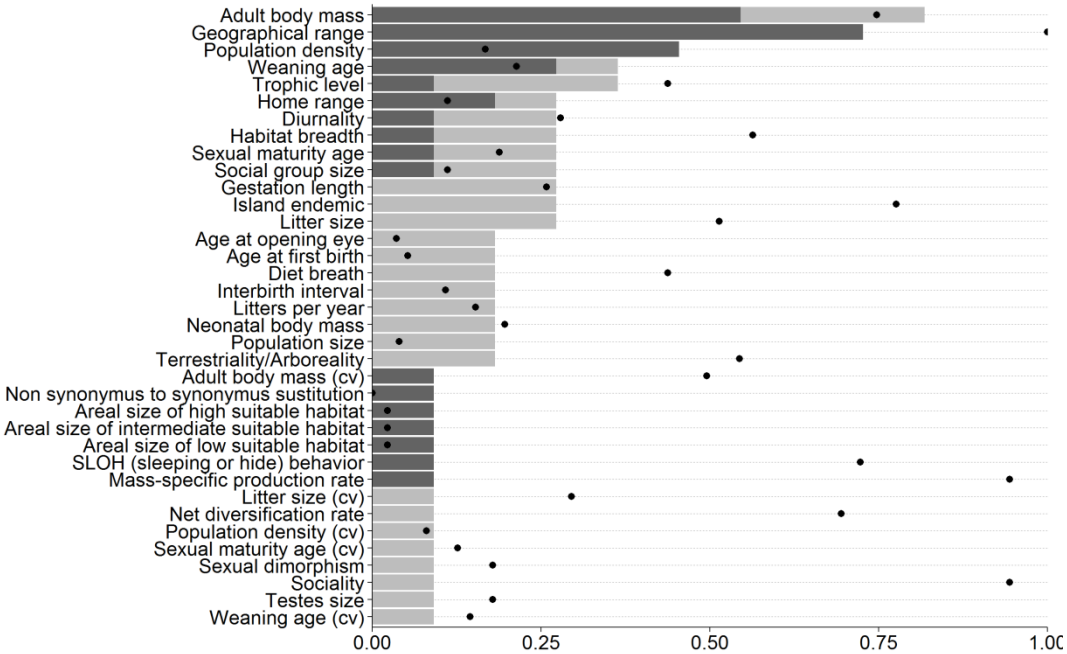

Figure 1.S1. Biological and ecological data availability, and frequency of association with extinction risk in terrestrial mammals. Length of bars represent the proportion of studies in which variables were considered (max=11). Dark filling represents studies in which variables significantly related to the threat status of mammals. Light filling represents studies in which variables did not relate to the threat status of mammals. Black circles symbolize the proportion of species with data for that trait in the database PanTHERIA (Jones et al. 2009) or self-obtained data employed in the cited studies, from the 4668 terrestrial mammals with data for at least one trait in PanTHERIA.

Table 1.S2. Description of intrinsic traits included in the analyses. *N*, number of terrestrial species with available estimates.

Trait	Definition provided in the data source reference	N	Data source
Adult body mass (g)	Mass of adult (or age unspecified) live or freshly-killed specimens (excluding pregnant females) using captive, wild, provisioned, or unspecified populations; male, female, or sex unspecified individuals; primary, secondary, or extrapolated sources; all measures of central tendency; in all localities.	3427	PanTHERIA (Jones et al, 2009)
Geographical range (km^2)	Calculated using IUCN distribution data with a cylindrical equal-area projection (ArcGIS 9.3).	4668	Spatial data of the IUCN Red List (IUCN

Trait	Definition provided in the data source reference	N	Data source
			2014)
Population density (n/km^2)	Number of individuals per square kilometer, estimated with either direct, indirect or unspecified counts, measured in any area size within a human, ecological or unspecified boundary, over any duration of time, using non-captive, non-provisioned populations; male, female, or sex unspecified individuals; primary, secondary, or extrapolated sources; all measures of central tendency; in all localities.	936	PanTHERIA (Jones et al, 2009)
Weaning age (days)	Age when primary nutritional dependency on the mother ends and independent foraging begins to make a major contribution to the offspring's energy requirements, measured as either weaning/lactation length, nutritionally independent, first solid food, last observed nursing, age at first flight (bats only), age at pouch exit or length of teat Attachment (marsupials only) or unspecified definition, using captive, wild, provisioned, or unspecified populations; male, female, or sex unspecified individuals; primary, secondary, or extrapolated sources; all measures of central tendency; in all localities.	1095	PanTHERIA (Jones et al, 2009)

Table 1.S3. Correlations between explanatory variables included in the intrinsic species-based model. Spearman's ρ values and sample sizes (in brackets) are provided.

	Population density	Geographic range	Weaning age
Geographic range	-0.14 (902)		
Weaning age	-0.57 (568)	-0.11 (1056)	
Body mass	-0.76 (899)	-0.08 (3088)	0.61 (1041)

Table 1.S4. Description of *anthromes* as in Ellis et al. (2010) .

Group	Biomes included	Description
Dense settlements	Urban	Urban and other dense settlements
	Mixed ettlements	Dense built environments with very high populations
Villages	Rice villages	Villages dominated by paddy rice
	Irrigated villages	Villages dominated by irrigated crops
	Rainfed villages	Villages dominated by rainfed agriculture
	Pastoral villages	Villages dominated by rangeland
Croplands	Residential irrigated croplands	Irrigated cropland with substantial human populations
	Residential rainfed croplands	Rainfed croplands with substantial human populations
	Populated rainfed cropland	Croplands with significant human populations, a mix of irrigated and rainfed crops
	Remote croplands	Croplands without significant populations
Rangeland	Residential rangelands	Rangelands with substantial human populations
	Populated rangelands	Rangelands with significant human populations
	Remote rangelands	Rangelands without significant human populations
Seminatural lands	Residential woodlands	Forest regions with minor land use and substantial populations
	Populated woodlands	Forest regions with minor land use and significant populations
	Remote woodlands	Forest regions with minor land use without significant populations
	Inhabited treeless and barren lands	Regions without natural tree cover having ony minor land use and a range of populations
	Wild woodlands	Forests and savanna
Wildlands	Wild treeless and barren lands	Regions without natural tree cover (grasslands, shrublands, tundra, desert and barrend lands)

Table 1.S5. Terrestrial mammal species excluded from the anthropogenic models (PGLS) due to topological errors (their geographic ranges were covered by *anthromes* in less than 95% of their total surface; N=86). *Thr,.* indicates if the species is thereatened (1) or not (0); the following columns represent the overlapping proportion of the geographic range with each *anthrome* class: *D,* dense settlements; *V*, villages; *C*, croplands; *R*, rangelands; *S.N.*, semi-natural lands; *W*, wildlands; *Addition,* of all previous classes.

Species name	Thr.	D	V	C	R	S.N.	W	Addition
Abrothrix hershkovitzi	0	0	0	0	0	0	0.92	0.92
Acerodon humilis	1	0.22	0	0.02	0	0.71	0	0.95
Aethomys kaiseri	0	0.01	0.05	0.11	0.34	0.42	0.02	0.95
Allactodipus bobrinskii	0	0	0.01	0.02	0.74	0.01	0.12	0.90
Alopex lagopus	0	0	0	0	0.01	0.06	0.82	0.89
Ardops nichollsi	0	0.03	0	0.42	0.05	0.44	0	0.95
Babyrousa togeanensis	1	0	0	0	0	0.92	0	0.92
Bettongia lesueur	0	0	0	0	0.24	0.14	0	0.39
Brachyphylla cavernarum	0	0.41	0.03	0.21	0.06	0.25	0	0.95
Chilonatalus tumidifrons	0	0	0	0	0	0.5	0.41	0.91
Chiroderma improvisum	1	0.01	0	0.37	0.16	0.4	0	0.94
Crocidura jacksoni	0	0.02	0.2	0.23	0.4	0.06	0.02	0.93
Crocidura orii	1	0.12	0	0	0	0.82	0	0.94
Crocidura watasei	0	0.2	0.04	0.03	0	0.63	0	0.90
Dasyprocta coibae	1	0	0	0	0	0.07	0.5	0.57
Dicrostonyx groenlandicus	0	0	0	0	0	0.02	0.9	0.92
Dicrostonyx torquatus	0	0	0	0	0	0.06	0.88	0.94
Dipodomys insularis	1	0	0	0	0.05	0.51	0	0.57
Dipodomys margaritae	1	0	0	0	0	0	0.03	0.03
Dobsonia pannietensis	0	0.08	0	0	0	0.84	0.02	0.95
Echymipera davidi	1	0	0	0	0	0.76	0	0.76
Emballonura semicaudata	1	0	0	0.02	0	0.05	0.25	0.32
Enhydra lutris	1	0	0	0	0	0.01	0.02	0.03
Geocapromys ingrahami	1	0	0	0	0	0	0	0
Hippocamelus bisulcus	1	0	0	0	0.34	0.15	0.43	0.93
Lagorchestes hirsutus	1	0	0	0	0	0	0	0
Lemmus sibiricus	0	0	0	0	0	0.03	0.9	0.93
Leontopithecus caissara	1	0	0	0.2	0.5	0.06	0	0.76
Leporillus conditor	1	0	0	0	0	0	0	0
Lepus arcticus	0	0	0	0	0	0.04	0.82	0.86
Lepus flavigularis	1	0	0	0.39	0.48	0	0	0.87
Lepus insularis	0	0	0	0	0.04	0	0	0.04
Lontra felina	1	0	0	0	0.04	0.05	0.09	0.18
Lophuromys medicaudatus	1	0.13	0.36	0.13	0.09	0.24	0	0.94

Species name	Thr.	D	V	C	R	S.N.	W	Addition
Lophuromys woosnami	0	0.06	0.54	0.12	0.06	0.13	0.02	0.93
Melomys caurinus	1	0.22	0	0.02	0	0.71	0	0.95
Melomys talaudium	1	0.22	0	0.02	0	0.71	0	0.95
Mesocapromys angelcabrerai	1	0	0	0.37	0	0	0	0.37
Microtus abbreviatus	0	0	0	0	0	0	0.32	0.32
Miniopterus fuscus	1	0.18	0.06	0.03	0	0.67	0	0.94
Mirimiri acrodonta	1	0	0	0	0	0	0.06	0.06
Mormopterus acetabulosus	1	0.11	0.03	0.26	0	0.33	0	0.72
Mus triton	0	0.02	0.15	0.14	0.39	0.24	0.01	0.95
Mustela erminea	0	0.01	0.02	0.17	0.12	0.15	0.48	0.95
Myonycteris brachycephala	1	0	0	0.2	0	0.74	0	0.94
Myotis vivesi	1	0	0	0	0.69	0.14	0.01	0.83
Myotis yanbarensis	1	0.21	0	0	0	0.63	0	0.84
Mysateles gundlachi	1	0	0	0.27	0.01	0.49	0.06	0.84
Mysateles meridionalis	1	0	0	0	0	0.67	0.18	0.85
Natalus primus	1	0	0.02	0.4	0.01	0.43	0.06	0.91
Nesoryzomys swarthi	1	0	0	0	0	0	0.51	0.51
Notomys aquilo	1	0	0	0	0.77	0.01	0.02	0.8
Octodon pacificus	1	0	0	0	0	0.9	0	0.9
Oligoryzomys magellanicus	0	0	0	0	0.58	0.03	0.32	0.93
Ovibos moschatus	0	0	0	0	0	0.03	0.85	0.89
Peromyscus keeni	0	0.01	0	0.01	0.02	0.25	0.65	0.94
Peromyscus pseudocrinitus	1	0	0	0	0.92	0	0	0.92
Phyllomys thomasi	1	0	0	0	0.76	0.15	0	0.91
Pipistrellus maderensis	1	0.03	0	0.08	0.64	0.1	0	0.85
Potorous gilbertii	1	0	0	0	0.04	0	0	0.04
Pseudomys fieldi	1	0	0	0	0	0	0	0
Pteropus faunulus	1	0	0	0.15	0	0.36	0	0.5
Pteropus fundatus	1	0.01	0	0	0	0.68	0	0.69
Pteropus livingstonii	1	0.14	0	0.73	0	0.01	0	0.88
Pteropus melanotus	1	0	0.23	0.52	0	0.16	0	0.91
Pteropus niger	1	0.12	0	0.15	0	0	0	0.27
Pteropus nitendiensis	1	0	0	0.57	0	0	0	0.57
Pteropus pohlei	1	0.03	0	0.02	0	0.9	0	0.95
Pteropus rennelli	1	0	0	0	0	0.78	0.01	0.79
Pteropus seychellensis	0	0.06	0.07	0.53	0.05	0.03	0.14	0.87
Rattus simalurensis	1	0	0.07	0.33	0	0.03	0	0.43
Rattus stoicus	1	0	0	0.61	0	0.18	0	0.79
Rhinolophus ruwenzorii	1	0.03	0.37	0.23	0.11	0.2	0.01	0.95
Sorex jacksoni	0	0	0	0	0	0.04	0.83	0.87

Species name	Thr.	D	V	C	R	S.N.	W	Addition
Stenoderma rufum	1	0.63	0.04	0.05	0.06	0.14	0	0.94
Sturnira thomasi	1	0.01	0	0.37	0.16	0.4	0	0.94
Sylvilagus mansuetus	0	0	0	0	0.13	0.59	0	0.72
Sylvisorex johnstoni	0	0.02	0.1	0.11	0.17	0.36	0.17	0.94
Tadarida bemmeleni	0	0.02	0.2	0.2	0.32	0.14	0.03	0.91
Tadarida bregullae	1	0	0	0.05	0	0.83	0.03	0.91
Tadarida tomensis	1	0.08	0	0.25	0	0.6	0	0.94
Taterillus lacustris	0	0	0.03	0.86	0.01	0.05	0	0.95
Tokudaia tokunoshimensis	1	0	0	0	0	0.83	0	0.83
Tragulus nigricans	1	0	0	0.17	0	0.63	0	0.80
Urocyon littoralis	1	0	0	0.05	0.21	0	0.13	0.40
Ursus maritimus	1	0	0	0	0	0.02	0.26	0.28

Table 1.S6. Correlations between explanatory variables included in the extrinsic species-based model (N=4348). Spearman's ρ values are provided.

	Urban	Villages	Croplands	Rangelands	Semi-natural lands
Villages	0.21				
Croplands	0.03	0.14			
Rangelands	-0.24	-0.32	-0.30		
Semi-natural lands	0.01	-0.19	-0.28	-0.60	
Wildlands	-0.14	-0.25	-0.29	-0.22	0.04

Table 1.S7. Correlations between all explanatory variables included in both the intrinsic and extrinsic species-based models (o*nly species with information for both types of variables are considered*). Spearman's ρ values and sample sizes (in brackets) are provided.

	Urban	Villages	Croplands	Rangelands	Semi-natural lands	Wildlands	Geographic range	Body mass	Populaion density
Villages	0.53								
	(4339)								
Croplands	0.39	0.49							
	(4339)	(4339)							
Rangelands	-0.33	-0.20	-0.20						
	(4339)	(4339)	(4339)						
Semi-natural	0.18	-0.06	-0.20	-0.59					
lands	(4339)	(4339)	(4339)	(4339)					
Wildlands	-0.10	-0.31	-0.26	-0.08	0.30				
	(4339)	(4339)	(4339)	(4339)	(4339)				
Geographic	0.11	0.12	0.11	0.15	0	0.53			
range	(4339)	(4339)	(4339)	(4339)	(4339)	(4339)			
Body mass	-0.11	-0.06	-0.10	-0.03	0.07	-0.01	-0.09		
	(3017)	(3017)	(3017)	(3017)	(3017)	(3017)	(3017)		
Populaion	0.25	-0.12	0.16	0.05	-0.19	-0.03	-0.13	-0.76	
density	(876)	(876)	(876)	(876)	(876)	(876)	(876)	(868)	
Weaning	-0.15	0.03	-0.14	-0.03	0.15	-0.03	-0.11	0.60	-0.57
age	(1023)	(1023)	(1023)	(1023)	(1023)	(1023)	(1023)	(1006)	(545)

Appendix 1.S2. Species-based models: complementary results

Intrinsic predictors of vulnerability

Table 1.S8. Results of the intrinsic PGLS including all mammals with available data. *Model I1* is presented in the main manuscript. *Models I1, I3 and I4* exclude species classified as threatened following criterion B. *Model I2* includes all species with available data for the presented variables. *Model I4* includes all terrestrial mammals in the IUCN Red List after imputation of data for missing traits. *β,* coefficient estimates; *SE*, standard errors of the coefficients.

Traits	Model I1 (N=981)	Model I2 (N=1027)	Model I3 (N=2747)	Model I4 (N=3595)
	β (SE)	β (SE)	β (SE)	β (SE)
Geographic range	-0.45 (0.028)***	-	-0.44 (0.015)***	-0.42 (0.014)***
Weaning age	0.26 (0.127)*	0.31 (0.147)*	-	-0.27 (0.066)***
Body mass	0.29 (0.047)***	0.28 (0.052)***	0.31 (0.031)***	0.28 (0.033)***
Adjusted R^2	0.25	0.06	0.25	0.22

*** p<0.001; ** p<0.01; * p<0.05

Note about the imputation technique

The results thrown by model I4 (Table 1.S8) show that weaning age negatively relate to threat status, i.e. terrestrial mammals with a later maturation are less likely to be threatened. This contradicts previous studies and is biologically unlikely (e.g. Davidson et al. 2009; Marco et al. 2014). Imputed data to fit model I4 were obtained based on the available $\log_{10}$-transformed data for geographic range (sq·km), weaning age (days) and body mass (g) and the supertree of Bininda-Emonds et al. (2007) presented by Fritz et al. (2009); using the *phylopars* and *phylopars.predicts* functions from the 'Rphylopars' package (Goolsby et al. 2015) in R (R Core Team 2014).

To further understand these results, we additionally followed the same procedure but using a more complete database including the three mentioned traits plus population density (excluded from the analyses due to its correlation with body mass). Results from these two different imputation processes are quite different (Fig. 1.S2), especially for those variables with less available data like weaning age (Fig. 1.S2c).

This suggests that imputed values are highly dependent on the initial subset of variables from which the function imputes data and call for caution when interpreting results.

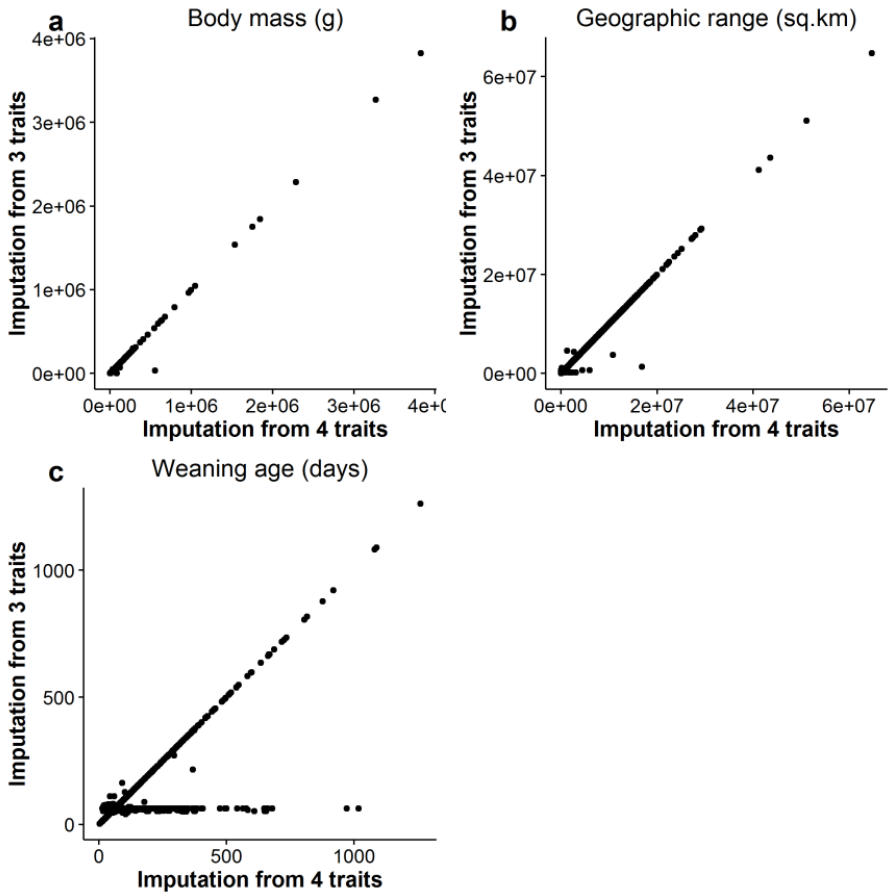

Figure 1.S2. Linear regression between the imputed values of the three intrinsic predictors of vulnerability, based on 4 traits in the original data set (X-axis) and based on 3 traits in the original data set (Y-axis).

Anthropogenic predictors of vulnerability

Table 1.S9. Results of the anthropogenic PGLS for all mammals. *Model A1* is included in the main manuscript, including all mammals with available distribution data and phylogenetic information. *Model A2* includes the same species as the main model fitted for intrinsic traits (*Model I1,* Table 1.S8), except from four species which geographic range did not overlap with the *Anthromes* geographic data (Table 1.S5). *β,* coefficient estimates; *SE*, standard errors of the coefficients.

Anthromes	Model A1 (N=3908)	Model A2 (N=977)
	β (SE)	β (SE)
Villages	0.00 (0.01)	-0.01 (0.015)
Croplands	0.08 (0.012)***	0.09 (0.027)***
Rangelands	0.00 (0.009)	-0.02 (0.019)
Semi-natural	0.22 (0.012)***	0.20 (0.029)***
Wildlands	-0.17 (0.009)***	-0.13 (0.021)***
Adjusted R^2	0.13	0.07

*** p<0.001; ** p<0.01; * p<0.05

Intrinsic and anthropogenic predictors of vulnerability

Table 1.S10. Results of the PGLS including both intrinsic and anthropogenic variables for all mammals. *β,* coefficient estimates; *SE*, standard errors of the coefficients. (N=955)

Traits	β (SE)
Geographic range	-0.43 (0.034)***
Weaning age	0.25 (0.126)*
Body mass	0.25 (0.048)***
Villages	0.02 (0.014)
Croplands	0.09 (0.024)***
Rangelands	-0.04 (0.017)*
Semi-natural	0.05 (0.029)
Wildlands	-0.03 (0.021)
Adjusted R^2	0.25

*** p<0.001; ** p<0.01; * p<0.05

Appendix 1.S3. Spatial predictions: data & results

The gridded distribution of mammals was obtained by overlapping a 1x1º grid with every species geographic range in ArcView 3.2. (ESRI 1999). Grids were projected in Eckert IV (equal area) to match the projection of the land use original data source (see below). Therefore, not all grids have the same area, ranging from 1402 km² (in the Poles) to 12391 km² (in the Equator). These differences in grid-cell size should not be a problem, since the only purpose of gridding the study area is to spatially represent predictions based on adjusted coefficients of previous fitted models at the species level. The nomenclature employed in this section follows the models on previous appendices.

Intrinsic vulnerability

As this is not a spatial parameter *per se*, different paths to estimate intrinsic vulnerability and map it can be followed. Previous studies have used the average prediction (based on life-history and ecological traits) for all species occurring within a certain grid cell (Cardillo et al. 2006), but this approach limits the analyses to species with data on all traits included in the model. Therefore, we explored an additional approach based on calculating the median value for all traits included in the model - aiming to represent the "average" mammal occurring within each grid cell- and predicted based on these values. This approach may produce combinations of traits that are not biologically realistic (e.g. late weaning age and small body size) but allows us to include information from as many species as possible. We also explore an approach based on average predictions and below we compare from both approaches.

On the first place, we predicted intrinsic vulnerability based on the median trait values per grid using the four versions of the intrinsic model. All the alternatives are displayed in figs. 1.S2a, 1.S2d, 1.S2g and 1.S2j (first column); with each row representing a different model from Table 1.S2 (*Models I1, I2, I3* and *I4,* respectively). These predictions show qualitatively the same, well-correlated results (Spearman's ρ, 0.72-0.99) with a moderate level of spatial coincidence among areas of high

vulnerability (50% of areas are classified as such independently of the model employed) and low vulnerability (51% of areas are classified as such independently of the model employed). Non-coincident areas were very rarely classified as the opposite (i.e. high vulnerability as low vulnerability areas or vice versa); they normally were considered as non-significant. Areas of high and low vulnerability were defined based on spatial autocorrelation clusters, calculated as local Moran's I values within queen neighbors grid-cells (positive significant correlation, $p<0.01$).

Secondly, we defined spatial intrinsic vulnerability (per grid cell) as the mean value of the predicted value for species occupying that area. The results from this approach are shown in figures 1.S2b, 1.S2e, 1.S2h and 1.S2k (second column). Differences among rows represent the various models used for prediction (*Models I1, I2, I3* and *I4,* respectively) that have relatively high correlation (Spearman's ρ, 0.54-0.85) and moderate coincidence among areas of high vulnerability (49% of areas are classified as such independently of the model employed) and low vulnerability (44% of areas are classified as such independently of the model employed).

Both approaches (prediction from median trait values and mean of species predictions) provide similar results (Table 1.S11), but as presented above, we found more differences among alternative models when averaging species predictions by grid cell than when using median values per grid cell. Thus, we focused on the approach based on median traits per grid cell and including more predictors in the main manuscript.

Table 1.S11. Correlations between intrinsic vulnerability predictions based on the same model, but using different calculations for their spatial representation (prediction from median trait values and mean of species predictions; first vs. second column in Fig. 1.S2). Spearman's ρ values are provided.

Species-based model	Spearman's ρ between predictions
I1	0.77
I2	0.81
I3	0.91
I4	0.91

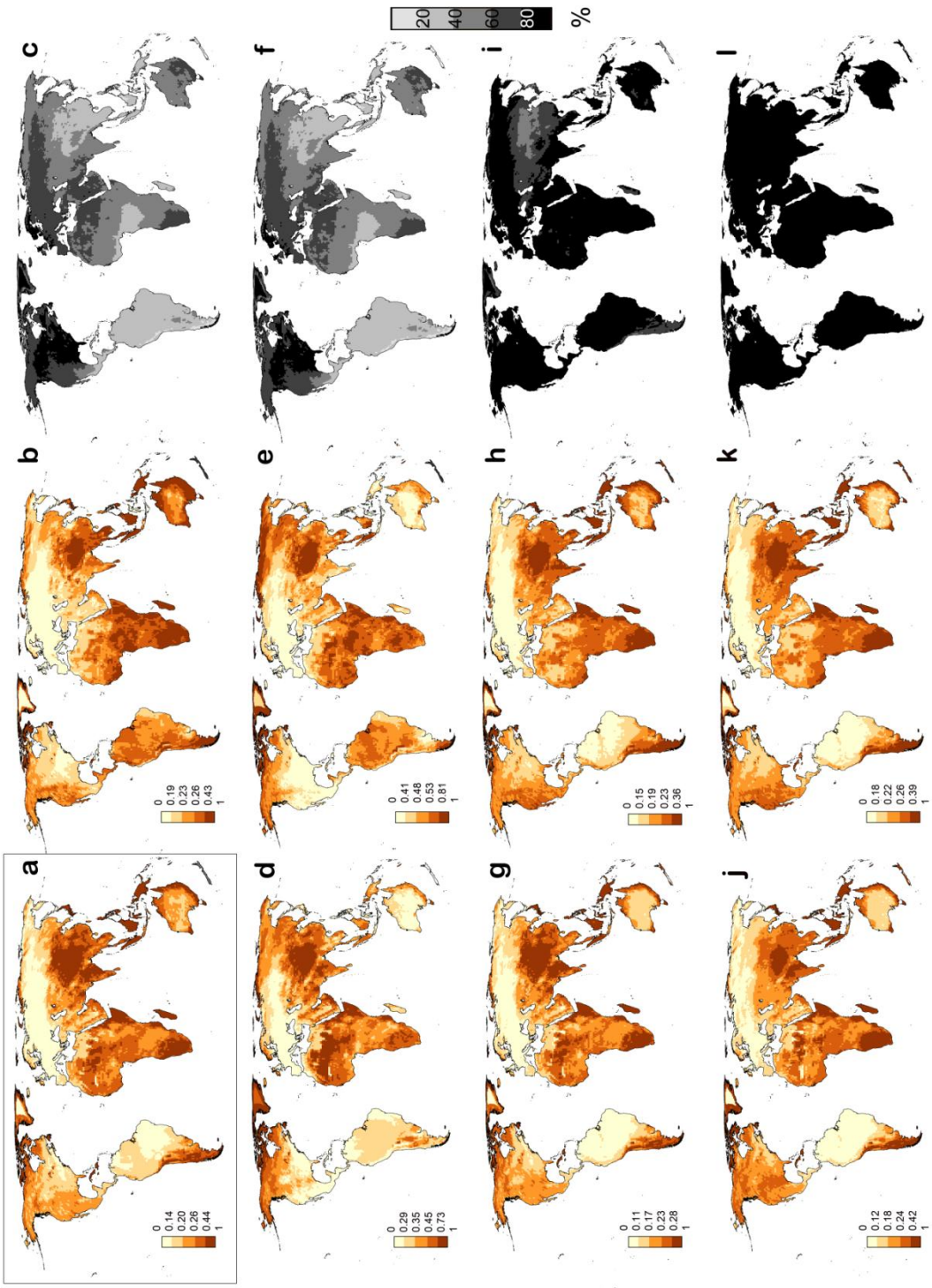

Figure 1.S3. Spatial intrinsic vulnerability calculated as the prediction from the median terrestrial mammal inhabiting each grid cell (a, d, g & j), and as the mean value of vulnerability per species occurring within a grid cell (b, e, h & k). First-row predictions (a & b) are based on *Model I1* (main manuscript), including geographic range, adult body mass and weaning age. Second row (d & e)

shows predictions from *Model I2*, combining adult body mass and weaning age. Third-row maps (g & h) are predicted using *Model I3:* adult body mass and geographic range. Last-row predictions are based on the model with imputed data (*Model I4)*, including the three traits (Table 1.S7). Percentage of available data (number of species for which data included in the models were available, over the total mammals known to be present in each grid cell) are presented in the last column (c, f, i & l), to show the uncertainty when mapping vulnerability in this way. All predictions (of continuous Red List Status) are standardized between 0-1 to facilitate comparison, and divided by data quantiles, with darker colors indicating higher vulnerability. Map of data availability presents equal breaks, as indicated on the legend. Framed map shows the version included in the main text.

Extrinsic vulnerability

Species-based models were adjusted based on two different subgroups of terrestrial mammals, one including all species with available information (*Model A1)* and the other including only species included in the intrinsic species-based model (*Model A2)*. Spatial predictions on Figs. 1.S3a and 1.S3b correspond to *Model A1*, whereas predictions of Figs. 1.S3c and 1.S3d are based on *Model A2.* Differences between maps on the left (1.S3a and 1.S3c) and right columns (1.S3b and 1.S3d) are consequence of the method used to define extrinsic vulnerability at the grid-cell level. In the first case, grid cells are considered "new species" for which percentage of land covered by the different *anthromes* per grid cell are the new explanatory variables. In the second case, extrinsic vulnerability is calculated as the mean extrinsic vulnerability, predicted for all species occurring within a grid cell (for comparison with the approach explored for intrinsic traits).

There is high coincidence between *Model A1* (S3a) and *Model* A2 (S3c), with a Spearman's rank correlation coefficient (ρ) of 0.97. Areas of high extrinsic vulnerability (calculated as univariate local Moran's I) coincide in 83% of cases, and low extrinsic vulnerability is assigned equally with both models in 84% of cases. Results are thus, not very sensitive to differences in the subset of species included in model A1 versus A2.

In the case of predictions made by averaging the individual extrinsic vulnerabilities of all species inhabiting each grid cell, results from the model including all species and the one including only those with intrinsic information available (S3b

vs. S3d) are not that similar, despite a high Spearman's rank correlation value (ρ = 0.94). Areas of high extrinsic vulnerability coincide in 76% of cases, while low vulnerability clusters only coincide in 33% of cases. Areas of high vulnerability are relatively persistent, whereas many low intrinsic vulnerability areas disappear when considering only a subset of species (Fig. 1.S3d).

In general, differences among methods to spatially represent extrinsic vulnerability are not large (Table 1.S12). However, areas of high and low vulnerability substantially vary depending on the employed method to spatially predict. Hence, it is not trivial to choose one approach or the other. In our case, we believe predicting based on the actual cover is more informative and allows to pick more restricted areas, without the limitation of the "buffer effect" (consequence of the nature of species' geographic ranges) that appears in cases b and d (Fig. 1.3S).

Table 1.S12. Correlations between extrinsic vulnerability predictions based on the same model, but using different calculations for spatial representation (prediction from median trait values and mean of species predictions; first vs. second column in Fig. 1.S3). Spearman's ρ values are provided.

Species-based model	Spearman's ρ between predictions
A1	0.60
A2	0.60

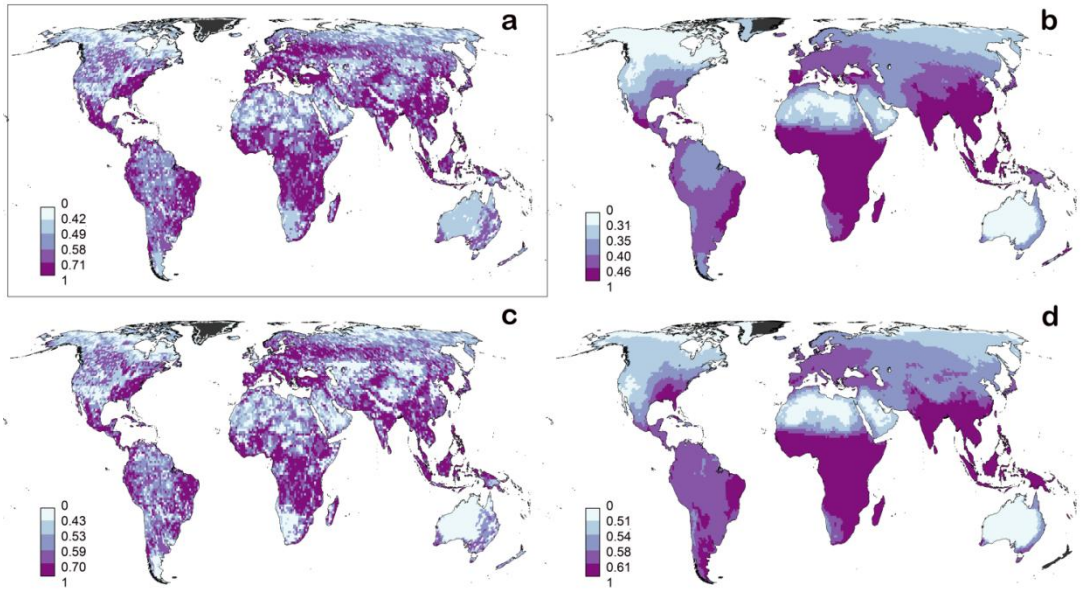

Figure 1.S4. Spatial extrinsic vulnerability calculated as the prediction from the proportion of *anthromes* occurring within each grid cell (a & c), and as the mean value of vulnerability per species occurring within a grid cell (b & d). First-row predictions (a & b) are based on *Model A1* (main manuscript), and the alternative including the same species as the main intrinsic model (c & d; *Model A2*; Table 1.S8). All predictions (of continuous Red List Status) are standardized between 0-1 to facilitate comparison; legend's categories follow quantiles' division. Darker colors indicate higher vulnerability. Black areas indicate no data. Framed map shows the version included in the main text.

Zonation

Zonation is based on areas where high values of high/low intrinsic and extrinsic vulnerability coexist (positive spatial autocorrelation) or counteract (negative spatial autocorrelation) each other. In the main manuscript we presented the map of zones based on all terrestrial mammals, and also two separate zonations for small (≤3kg) and large mammals (>3 kg). As expected, the delimination of these areas varies depending on the subset of species analyzed.

Tables 1.S13 to 1.S15 present a description of the main characteristics of the identified zones including species' trait data availability, mammalian richness, and number of threatened mammals. In addition, we have included descriptive maps to illustrate the predominant *anthromes'* classes within each of the zone categories based on all mammals (Fig. 1.S5), only small (Fig. 1.S6) and only large mammals (Fig. 1.S7).

Table 1.S13. Summary of the available information for the traits employed to calculate intrinsic vulnerability, and numbers of threatened and total mammalian richness, global and segregated by zone category. Calculations are based on all terrestrial mammal species (N=5237). *Mean* refers to the mean number of mammals with available information by grid cell, *%* is that number divided by the total mammalian richness by grid cell; *Min-max* shows the minimum and maximum number of mammals with information by grid cell. *N* indicates the number of grid cells included in that zone.

Variable	Global (N=17474)			Double-susceptibility (N=2068)			Intrinsic-susceptibility (N=2370)			Extrinsic-susceptiblity (N=2945)			Low-susceptibility (N=2530)		
	Mean	% r	Min-max	Mean	% r	Min-max	Mean	% r	Min-max	Mean	% r	Min-max	Mean	% r	Min-max
Species knowledge															
geographic range	55.7	100%	1 - 252	86.4	100%	1 - 252	22.0	100%	1 - 141	84.5	100%	1 - 241	48.2	100%	1 - 233
body mass	48.4	87%	1 - 213	71.9	83%	1 - 213	19.3	88%	1 - 114	74.6	88%	1 - 211	43.4	90%	1 - 203
weaning age	27.9	50%	1 - 104	35.0	41%	1 - 103	13.9	63%	1 - 70	39.7	47%	1 - 101	25.0	52%	1 - 66
Threatened species	2.6	5%	0 - 40	6.7	8%	0 - 38	1.6	7%	0 - 25	2.8	3%	0 - 20	1.3	3%	0 - 16
Data deficient species	1.3	2%	0 - 20	2.3	3%	0 - 20	0.2	1%	0 - 9	2.7	3%	0 - 20	1.1	2%	0 - 16
Richness	55.7	-	1 - 252	86.4	-	1 - 252	22.0	-	1 - 141	84.5	-	1 - 241	48.2	-	1 - 233

‡‡ *100% availability is inherent to the nature of the analysis. If there is not information about geographic range, the species cannot enter the model.*

Table 1.S14. Summary of the available information of the selected traits employed to calculate intrinsic vulnerability, and numbers of threatened and total mammalian richness, global and segregated by zone category. Calculations are based on species smaller or equal than 3kg (N=2773). *Mean* refers to the mean number of mammals with available information by grid; *%* is that number divided by the total mammalian richness by grid cell; *range* shows the minimum and maximum number of mammals with information by grid cell. *N* indicates the number of grid cells included in that zone.

Variable	Global N=16699)			Double-susceptibility (N=3165)			Intrinsic-susceptibility (N=651)			Extrinsic-susceptiblity (N=1768)			Low-susceptibility (N=4808)		
	Mean	% r	Min-max	Mean	% r	Min-max	Mean	% r	Min-max	Mean	% r	Min-max	Mean	% r	Min-max
Species knowledge															
geographic range	36.3	100%	1 - 178	50.7	100%	1 - 178	28.1	100%	1 - 138	44.8	100%	1 - 142	16.6	100%	1 - 138
body mass	36.3	100%	1 - 178	50.7	100%	1 - 178	28.1	100%	1 - 138	44.8	100%	1 - 142	16.6	100%	1 - 138
weaning age	17.5	48%	1 - 58	20.4	40%	1 - 58	10.5	38%	1 - 54	23.1	52%	1 - 45	10.9	66%	1 - 37
Threatened species	0.6	2%	0 - 21	1.1	2%	0 - 17	1.4	5%	0 - 21	0.6	1%	0 - 6	0.0	0%	0 - 2
Data deficient species	0.6	2%	0 - 12	1.0	2%	0 - 12	0.9	3%	0 - 12	0.9	2%	0 - 9	0.0	0%	0 - 6
Richness	36.3	-	1 - 178	50.7	-	1 - 178	28.1	-	1 - 138	44.8	-	1 - 142	16.6	-	1 - 138

‡‡100% availability is inherent to the nature of the analysis. If there is not information about geographic range, the species cannot enter the model.

Table 1.S15. Summary of the available information of the selected traits employed to calculate intrinsic vulnerability and numbers of threatened, and total mammalian richness, global and segregated by zone category. Calculations are based on species larger than 3kg (N=538). *Mean* refers to the mean number of mammals with available information by grid; *%* is that number divided by the total mammalian richness by grid cell; *range* shows the minimum and maximum number of mammals with information by grid cell. *N* indicates the number of grid cells included in that zone.

Variable	Global (N=17183)			Double-susceptibility (N=1817)			Intrinsic-susceptibility (N=1796)			Extrinsic-susceptiblity (N=2614)			Low-susceptibility (N=2394)		
	Mean	% r	Min-max	Mean	% r	Min-max	Mean	% r	Min-max	Mean	% r	Min-max	Mean	% r	Min-max
Species knowledge															
geographic range	13.4	100%	1 - 60	21.5	100%	1 - 59	9.6	100%	1 - 53	12.0	100%	1 - 37	9.3	100%	1 - 31
body mass	13.4	100%	1 - 60	21.5	100%	1 - 59	9.6	100%	1 - 53	12.0	100%	1 - 37	9.3	100%	1 - 31
weaning age	10.8	81%	1 - 48	15.0	70%	1 - 46	8.1	84%	1 - 41	9.8	81%	1 - 26	8.1	87%	1 - 24
Threatened species	1.9	14%	0 - 49	6.2	29%	0 - 49	1.3	14%	0 - 38	1.2	81%	0 - 13	0.9	9%	0 - 6
Data deficient species	0.1	1%	0 - 3	0.1	0%	0 - 2	0.0	0%	0 - 2	0.3	10%	0 - 3	0.1	1%	0 - 3
Richness	13.4	-	1 - 60	21.5	-	1 - 59	9.6	-	1 - 53	12.0	-	1 - 37	9.3	-	1 - 31

‡‡100% availability is inherent to the nature of the analysis. If there is not information about geographic range, the species cannot enter the model.

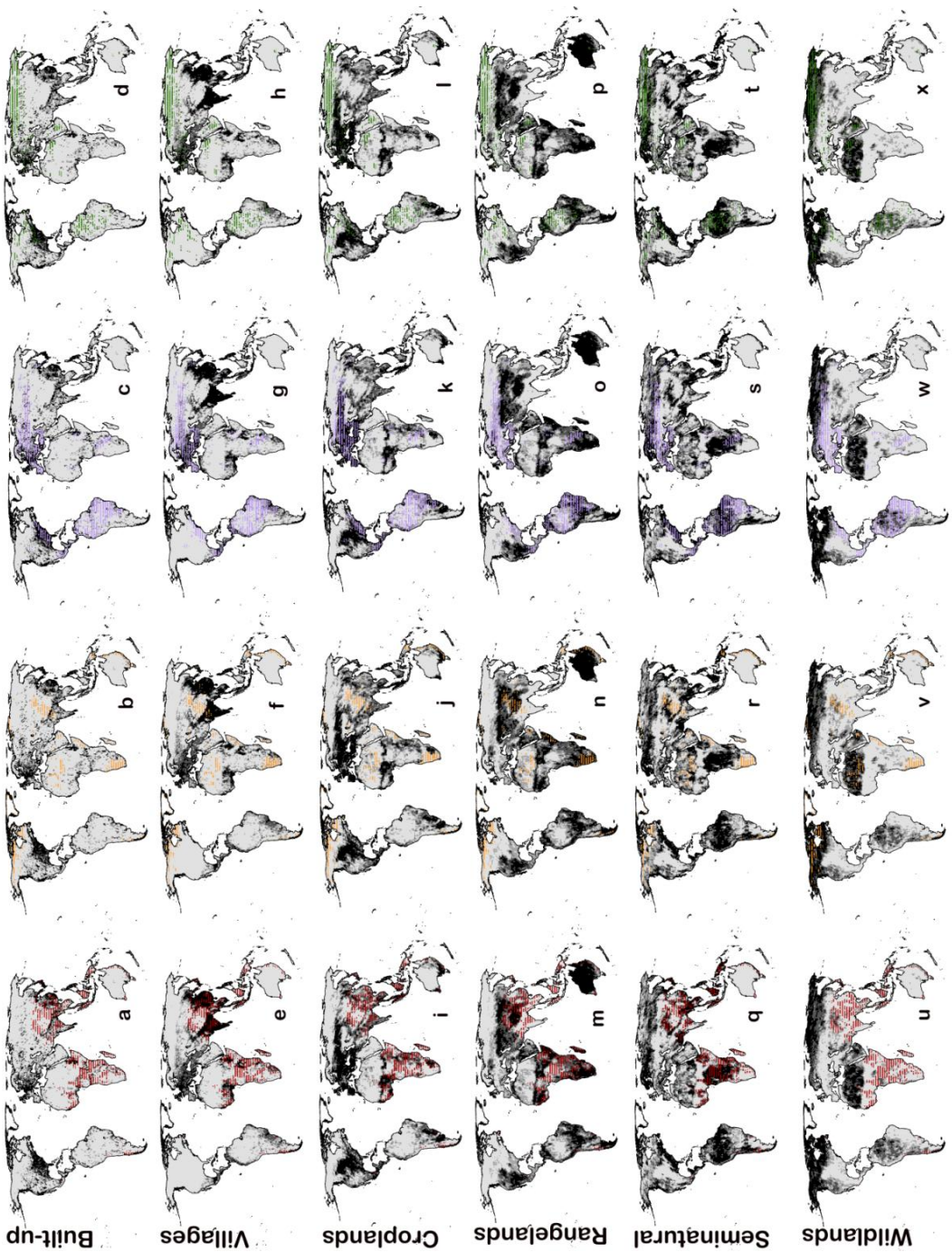

Figure 1.S5. Representation of the percentage per grid-cell covered by each of the six *anthromes*' categories (built-up areas, villages, croplands, rangelands, seminatural lands and wildlands), one in each row. Darker filling represents higher coverage of a certain *anthrome*. One zone category is overlapped in each column: double-susceptibility areas (panels a, e, i, m, q and u; red), intrinsic-susceptibility areas (panels b, f, j, n, r and v; orange), extrinsic-susceptibility areas (panels c, g, k, o, s and w; purple) and low-susceptibility areas (panels d, h, l, p, t and x; green). Zonation based on **all terrestrial mammals**.

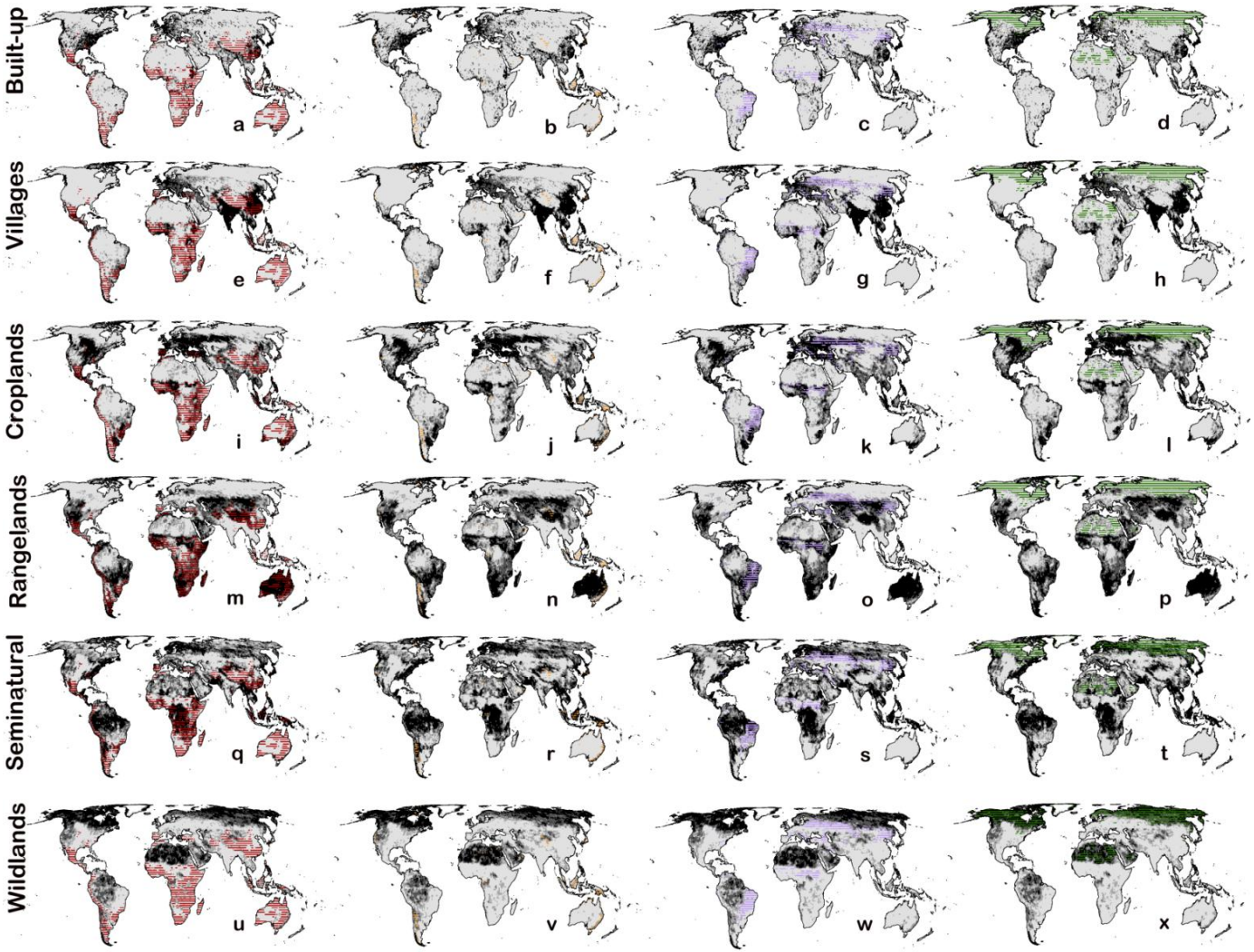

Figure 1.S6. Representation of the percentage per grid-cell covered by each of the six *anthromes*' categories (built-up areas, villages, croplands, rangelands, seminatural lands and wildlands), one in each row. Darker filling represents higher coverage of a certain *anthrome*. One zone category is overlapped in each column: double-susceptibility areas (panels a, e, i, m, q and u; red), intrinsic-susceptibility areas (panels b, f, j, n, r and v; orange), extrinsic-susceptibility areas (panels c, g, k, o, s and w; purple) and low-susceptibility areas (panels d, h, l, p, t and x; green). Zonation based on **terrestrial mammals smaller/equal than 3 kg**.

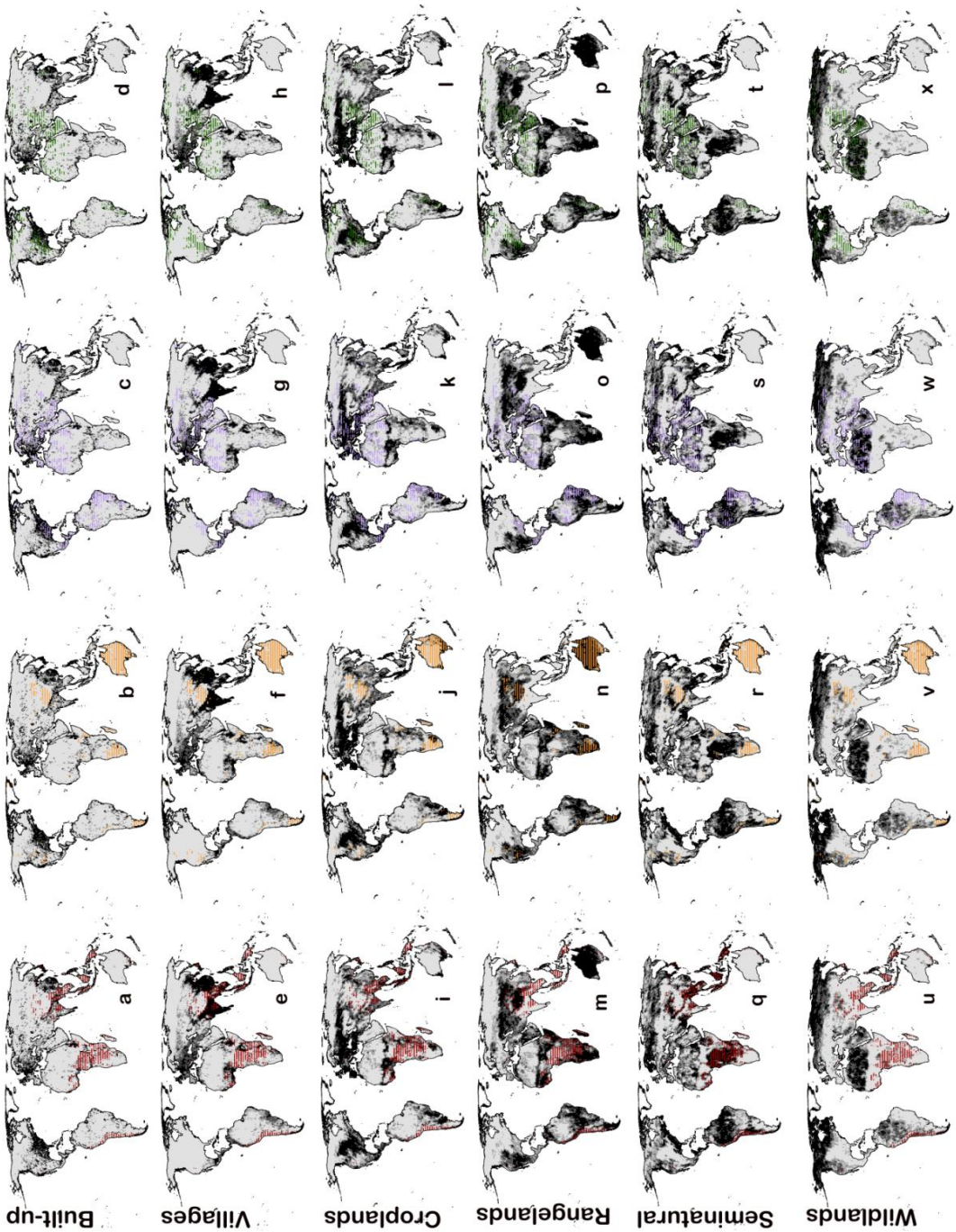

Figure 1.S7. Representation of the percentage per grid-cell covered by each of the six *anthromes*' categories (built-up areas, villages, croplands, rangelands, seminatural lands and wildlands), one in each row. Darker filling represents higher coverage of a certain *anthrome*. One zone category is overlapped in each column: double-susceptibility areas (panels a, e, i, m, q and u; red), intrinsic-susceptibility areas (panels b, f, j, n, r and v; orange), extrinsic-susceptibility areas (panels c, g, k, o, s and w; purple) and negligible-susceptibility areas (panels d, h, l, p, t and x; green). Zonation based **on terrestrial mammals larger than 3 kg**.

Socioeconomic correlates of gobal mammalian conservation status

Polaina, E., González-Suárez, M., and Revilla, E. (2015) Socioeconomic correlates of global mammalian conservation status. Ecosphere **6**:146. DOI: 10.1890/ES14-00505.1

Abstract

The main causes of biodiversity decline are related to human use of resources, which is ultimately triggered by the socioeconomic decisions made by individuals and nations. Characterizing the socioeconomic attributes of areas in which biodiversity is most threatened can help us identify decisions and conditions that promote the presence or absence of threats and potentially suggest more sustainable strategies. In this study we explored how diverse indicators of social and economic development correlate with the conservation status of terrestrial mammals within countries, explicitly exploring hypothesized linear and quadratic relationships. First, comparing countries with and without threatened mammals we found that those without threatened species are a disparate group formed by European countries and Small Island Developing States (SIDS) with little in common besides their slow population growth and a past of human impacts. Second, focusing on countries with threatened mammals we found that those with a more threatened mammalian biota have mainly rural populations, are predominantly exporters of goods and services, receive low to intermediate economic benefits from international tourism, and have medium to high human life expectancy. Overall, these results provide a comprehensive characterization of the socioeconomic profiles linked to mammalian conservation status of the world's nations, highlighting the importance of transborder impacts reflected by the international flux of goods, services and people. Further studies would be necessary to unravel the actual mechanisms and threats that link these socioeconomic profiles and indicators with mammalian conservation. Nevertheless, this study presents a broad and complete characterization that offers testable hypotheses regarding how socioeconomic development associates with biodiversity.

Resumen

Las principales causas del declive de la biodiversidad están relacionadas con el uso humano de recursos, el cual es provocado en último término por la toma de decisiones de carácter socioeconómico, que llevan a cabo individuos y naciones. Caracterizar los atributos socioeconómicos de áreas donde la biodiversidad se encuentra más amenazada puede ayudarnos a identificar condiciones que promueven la mayor o menor presencia de amenazas y, potencialmente, sugerir estrategias más sostenibles. En este estudio exploramos cómo diversos indicadores de desarrollo social y económico se correlacionan con el estado de conservación de mamíferos terrestres dentro de cada país, explorando explícitamente relaciones lineales y cuadráticas. En primer lugar, al comparar países con y sin mamíferos amenazados, encontramos que aquellos sin especies amenazadas son un grupo dispar formado por países europeos y pequeños estados-isla en vías de desarrollo (SIDS, por sus siglas en inglés) con poco en común aparte de su lento crecimiento poblacional y un pasado de considerable presión humana. En segundo lugar, centrándonos en países con alguna especie amenazada, encontramos que aquellos con más mamíferos amenazados se caracterizan fundamentalmente por tener poblaciones rurales, ser exportadores de bienes y servicios, recibir bajos-medios beneficios económicos derivados del turismo internacional, y tener esperanzas de vida intermedias-altas. En general, nuestros resultados proporcionan una caracterización de los perfiles socioeconómicos asociados a diferentes estados de conservación de mamíferos en las naciones del mundo, destacando la importancia de los impactos transfronterizos reflejados en el flujo internacional de bienes, servicios y personas. Estudios adicionales serían necesarios para resolver de manera concreta los mecanismos y amenazas que se esconden tras estos perfiles socioeconómicos, y que repercuten en el estado de conservación de los mamíferos. Sin embargo, este estudio presente una caracterización completa que ofrece hipótesis comprobables sobre la relación entre desarrollo socioeconómico y biodiversidad.

Introduction

Biodiversity loss has accelerated in recent times and many voices argue that we may be entering the Earth's 6th mass extinction event (Barnosky et al. 2012). The main threats to biodiversity are human-induced and include habitat loss, fragmentation, overexploitation, spread of exotic species and diseases, pollution, and climate change (Soulé 1991; Millenium Ecosystem Assessment 2005). Understanding why distinct species and sites are vulnerable to extinction is essential to reduce biodiversity losses occurring now and those that will likely occur in the future (Hoffmann et al. 2010b).

Comparative studies of extinction risk have focused on identifying differences in vulnerability at the species (or taxonomic group) level. These studies have associated species' vulnerability with a diversity of life-history and ecological factors, such as body size, geographic range size, ecological and social specialization, and phylogenetic-lineage in mammals (Cardillo et al. 2008; Davidson et al. 2009; González-Suárez & Revilla 2013) and other taxa (Webb et al. 2002; Cushman 2006). However, species-focused studies have been criticized for their lack of applicability to management and for ignoring the role of distinct threats (Cardillo & Meijaard 2012; Murray et al. 2014; but see Owens & Bennett 2000; González-Suárez & Revilla 2014). An attempt to overcome these weaknesses has been to explore human activities (which are potentially manageable) occurring within each species' geographic ranges. Studies using this approach have found that more endangered species tend to overlap with mosaic villages and residential croplands, densely populated areas or with increasing human population growth (Harcourt & Parks 2003; Pekin & Pijanowski 2012).

Species' intrinsic traits make some taxa more vulnerable to extinction, but also there are inherent properties associated with particular areas that make them more likely to harbor higher numbers of threatened species. The number of threatened species on a given site directly depends on the total species richness (how many species actually occupy that area) and the threats that affect those species (Fig. 2.1; Essl et al. 2013). In turn, species richness is determined by historical, biogeographical and environmental conditions, as well as by human activities that may have caused past local extinctions. Threats can include natural hazards (influenced by environmental

conditions, Fig. 2.1), but today the key threats for most species are of anthropogenic origin. For example, natural processes such as volcanoes, avalanches, or earthquakes are only considered to represent a threat for 1% of the 2551 terrestrial mammals with described threats, and these species are also at risk from anthropogenic activities (IUCN 2012a; González-Suárez & Revilla 2014). Human-related threats are associated with human activities which are mainly determined by socioeconomic development. Although analyzing the causes leading to observed development is beyond the scope of this study, it is worth noting that development is often influenced by environmental conditions (which in turn can be modified by development) and by the biogeographic history of a given area, both of which also influence its natural biodiversity. Eventually, if conditions change or nothing is done to stop it, threatened species become extinct (Fig. 2.1).

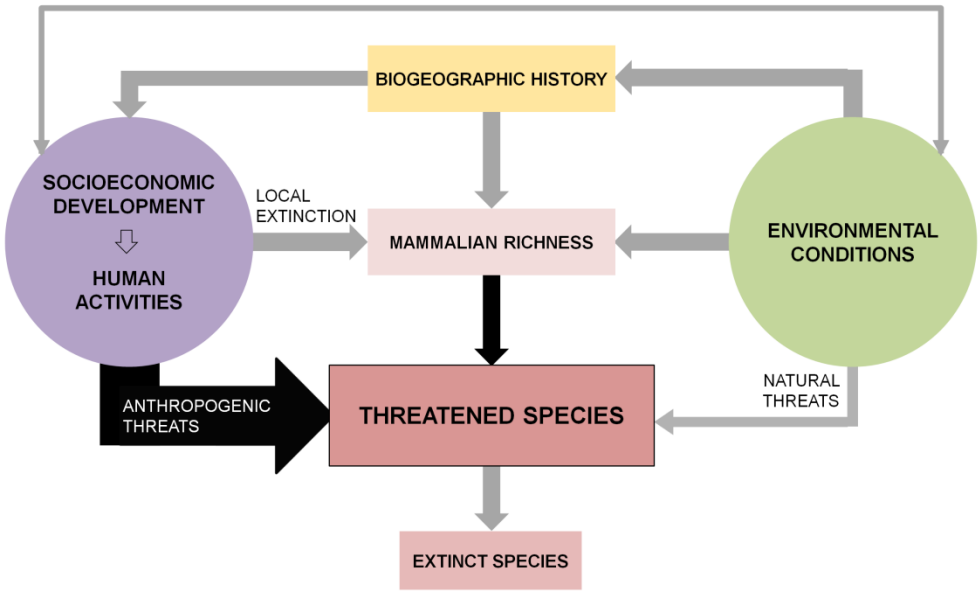

Figure 2.1. Conceptual framework describing the different factors that determine directly and indirectly the number of threatened species in an area at present. Black arrows represent anthropogenic processes explored in this paper.

Focusing on the spatial distribution of human threats, many studies have identified sensitive areas based on the correlation of different human pressure indicators and different measurements of biodiversity status. Since habitat destruction is one of the main causes of biodiversity decline, measurements of human land use are

those most-commonly employed to quantify human impact (Pimm & Raven 2000). In particular, conversion to arable land appears to be a key factor associated with greater risk at a regional and global scale (Kerr & Cihlar 2004; Lenzen et al. 2009; Lotz & Allen 2013). Another widely used indicator of human pressure is human population density, an aggregated proxy which has been positively correlated with abundance of threatened species at different scales (Burgess et al. 2007; Luck 2007). Within countries, some studies have shown that economic growth, energy use, human birth rate and different measures of national income or income inequality are associated with the number of threatened species (Kerr & Currie 1995; Hoffmann 2004; Holland et al. 2009; Naidoo & Adamowicz 2011) and with other measures of environmental damage (Grossman & Krueger 1995; Bradshaw et al. 2010). More recently, transborder impacts have also been suggested as risk factors found to be associated with the conservation status of the biota in developing countries (Meyfroidt et al. 2010; Lenzen et al. 2012).

While providing some insights, most of these past studies have only evaluated a few indicators at a time (but see Hoffmann 2004; Lotz & Allen 2013), without taking into account the many diverse aspects that describe socioeconomic development. This diversity is reflected, for example, in the 800 indicators included within the World Development Indicators book (World Bank Group 2005). One reason why past studies have focused on few indicators is that aside from population data, land use cover, and a few derived economic metrics, global socioeconomic data are only available at the country level, especially for indicators related to the trade of goods and services, and human life quality (CIESIN 2005; Nordhaus 2006; Asselen & Verburg 2012). Socioeconomic data do exist for finer political units (e.g. counties, states) in some areas, but in many cases data are not gathered or made public at such fine scales. Therefore, in order to conduct a global study that captures the diverse aspects of socioeconomic development, using country resolution is the most feasible solution. Country-based analyses are also relevant for management and policy implementation because political decisions influencing biodiversity at large scales are usually enacted at this level (Forester & Machlis 1996; Chape et al. 2005). Results from these analyses

can also be helpful to make countries aware of how their political, social and economic decisions may be influencing the conservation status of their biodiversity.

Here we present a comprehensive global analysis aimed to identify which indicators of socioeconomic development correlate with terrestrial mammalian conservation status at the country level. To explicitly include the diverse facets of socioeconomic development we considered indicators representing nine distinct categories defined by the World Bank (Table 2.S1) including those which have been previously linked to biodiversity status within countries (see references above). Some of the explored indicators can be more directly associated with threats (e.g., percentage of arable land) or benefits (e.g., number of protected areas) to biodiversity, while others are aggregated descriptors of development (e.g., human population density) which may capture more complex or indirect associations between socioeconomic processes, threats and biodiversity. Exploring this broad suite of indicators we first identified the socioeconomic characteristics that differentiate countries with and without threatened mammals. Then, considering only countries with threatened mammals, we determined which indicators are associated with higher relative richness of threatened mammals. In both sets of analyses we explicitly explored relationships proposed by the two general hypotheses relating socioeconomic development and environmental damage. The first hypothesis proposes a linear response, as human populations increase and become more industrialized the damages to biodiversity increase, with the greatest impacts associated with the most developed areas (e.g. Hettige et al. 2000; Clausen & York 2008). The second hypothesis proposes a quadratic relationship in which the greatest impacts occur at intermediate stages of development (inverted-U-shaped, or "Environmental Kuznets curve" as defined by Grossman & Krueger, 1995). Initially, population growth and industrialization would be associated with increased damages to biodiversity, but as societies become more technological and educated, they would also become more environmentally concerned and reduce their impact (Mcpherson & Nieswiadomy 2005). Because we explored different relationships and a broad range of indicators our results present a new global and comprehensive characterization of the key socioeconomic correlates of mammalian conservation status.

Methods

Socioeconomic indicators and species data

We used socioeconomic indicators compiled by the World Bank from different official sources grouped according to these simplified thematic categories: agriculture, economy, education, environment, health, infrastructure, labor and social protection, population and private sector (Table 2.S1). These categories were used in the analyses as non-redundant blocks, as explained below. Relative indicators (percentages and per capita values) were chosen over absolute values to facilitate comparison among nations. We used information from the year with the most available data in the last decade (year 2005) and excluded indicators considered a priori as relevant but with data available for <70% of the 204 countries in our database (9 indicators out of 39; Table 2.S2). As a result, no indicators from the categories education and infrastructure were included in our analyses. We did not use data imputation techniques for missing socioeconomic data because these data are not missing at random (e.g., more developed countries are more likely to have data on their development status), and the mechanisms by which data are missing can be complex and are not easily modeled (van Buuren 2012).

To assess the conservation status of terrestrial mammals we used the IUCN Red List of Threatened Species version 2012.1 (IUCN 2012b) which provides a single, global status for each species. Species defined as vulnerable, endangered or critically endangered are considered as threatened; whereas least concern or near threatened species are non-threatened. The 75 mammals classified as extinct in the wild or extinct were not included in the analyses since they cannot be classified in either category. Data deficient (DD) species were initially classified as non-threatened to define a conservative minimum estimate of threatened species per country. We then repeated the analyses considering DD species as threatened, and thus defining a maximum estimate of threatened species per country. Mammal presence within each country was determined using spatial data on the current (post 1980) global distribution of mammal species available from the IUCN (IUCN 2012b) selecting only native areas, with presence defined as extant or probably extant. We used a World Cylindrical

Equal Area projection in ArcGIS 10 (ESRI 2011) and intersected species ranges (N=5014) with a current global political map. All species with any portion of their range within the boundaries of a country were defined as present in that country.

Our approach to define the number of threatened species per country assumes that the global status of a species is potentially affected by human activities within each of the countries the species occupies. Ideally, mammalian status would have been defined using national assessments (to compare national socioeconomic development and status); however, this is not possible at a global scale. National assessments are not currently available for many countries and those available do not always follow standardized criteria, which prevents comparison. For example, only 23 countries have a National Red List according to the IUCN (<http://www.nationalredlist.org/>) and many include only partial assessments (Tables 2.S5 and 2.S6). Finally, we feel that the use of the global Red List to assess status is warranted if we consider that the responsibility of maintaining/menacing species should be shared by all countries that harbor them.

Analyses

First, we explored which socioeconomic indicators are associated with the presence (vs. absence) of threatened mammals using generalized linear models (GLMs). GLMs were fitted with the 'glm' procedure in R (R Development Core Team 2011) using a binomial family and a logit link. Second, considering countries with ≥1 threatened mammal we explored which indicators are associated the number of threatened species using the 'glm.nb' procedure in R (package MASS, Venables & Ripley 2002) with a negative binomial family and a log link. For both questions we tested linear and quadratic relationships for all indicators to account for the two main hypotheses mentioned in the introduction.

The variable selection procedure was the same for both analyses. First, we calculated pairwise Spearman's coefficients (ρ) and from any pair of highly correlated indicators (ρ> |0.8|) we excluded the indicator with fewer data available (7 excluded, out of 30; Tables 2.S2-2.S4). Using non-highly correlated indicators, we followed Purvis

et al. (2000) to define a minimum adequate model (MAM-based approach) for each socioeconomic category. We used this approach to maximize the use of available data, as some countries have available data for some indicators but not others and generating a complete dataset (removing all cases with any missing data) to analyze all categories at once would greatly limit the available sample size. MAMs by category were defined by starting with a full model including all indicators in the category from which the least significant variable was removed (one at a time), and then a new model (potentially with a different sample size) was fitted and evaluated. After finding a model containing only significant variables (using a conservative p-value=0.10) we retested the significance of previously removed variables and defined a MAM by category including any additional significant factors. Second, and in order to evaluate more systematically the relevance of the socioeconomic indicators, we determined indicator importance using an AIC_c-based approach. For this approach we were limited to the subset of countries with available data for all selected indicators in the category. We estimated variable importance for each socioeconomic indicator based on variable weights (Burnham & Anderson 2002) calculated from all possible model subsets in each category using the importance function in the MuMIn R-package (Barton 2013). We considered indicators were supported if their variable weights > 0.7. The final category model was defined using all variables included in the category MAM plus any additional variables identified as supported with the AIC_c-based approach. All variables included in the final category models were used to define a final global model using the same variable selection approaches (MAM- and AIC_c-based).

Model fit was estimated as the percentage of deviance explained. For the binomial model (presence of threatened mammals) we also calculated model sensitivity (true positive rate) and specificity (true negative rate; Allouche et al. 2006); setting an arbitrary 0.5 cut-off probability to define presences and absences. Furthermore, the area under the receiver operating characteristic curve (AUC) was calculated as a threshold-independent measure of model performance (Manel et al. 2001). To evaluate model predictive ability in the negative binomial model (abundance of threatened species) we calculated a standardized prediction error defined as the

number of threatened species predicted minus the observed number divided by total number of mammals. Positive errors indicate that the model overestimated the number of threatened mammals, whereas negative values indicate underestimation.

In addition to the tested socioeconomic indicators, all fitted models included as control variables (additional fixed effects) a country's total land area and its total mammalian richness. Including these variables allowed us to effectively model the association of socioeconomic indicators with the presence and number of threatened mammals per country controlling for the known effects of area and richness in the response variable (we can expect more threatened mammals in large countries inhabited by more mammals). An additional control variable, the mean number of mammals shared with neighboring countries (hereafter "shared mammals"), was included to account for the singularity of a country's fauna considering that nearby countries are generally more alike than those far apart. It is important to note that the number of shared mammals does not represent endemicity per se, but addresses issues of spatial autocorrelation among neighboring countries. It was calculated by identifying the number of species common to all pair of countries that share a border and then calculating the mean value over all neighbors for each country, standardized by the country's total mammalian richness. Harboring a higher percentage of shared mammals implies having a greater abundance of cosmopolitan species, generally less threatened but also potentially exposed to more sources of impact. Because islands have no neighboring countries, by definition they have 0% shared mammals.

Results

From the 204 countries with mammalian distribution range information and socioeconomic data, 168 host at least one globally threatened mammal (median=6 species, range 1-177), whereas 36 countries have none (Fig. 2.2a; Tables 2.S7 and 2.S8). From those 36, four countries contain DD species (median=1.5, range=1-4) that could potentially be threatened. Indonesia, Brazil, Mexico and India are the countries with the highest number of threatened mammals (649, 625, 454 and 352 species respectively if DD are considered as non-threatened).

Presence of threatened species

We found that diverse socioeconomic indicators are associated with the presence (vs. absence) of threatened mammals. Tourism receipts and urban population exhibit an inverted-U relationship with the probability of having threatened mammals. On the contrary, the percentage of arable land by country relates with the response variable following a positive parabola. Population growth presents a positive linear effect on the probability of containing threatened species by country (Table 2.1). Countries with no threatened mammals have either high or low percentages of urban population and international tourism receipt values, intermediate percentages of their territory are devoted to arable lands (extreme values are more common in countries with threatened mammals), and exhibit relatively slow population growth rates (Fig. 2.3). Classifying DD species as threatened did not qualitatively change these results except that the percentage of urban population was no longer a relevant indicator (Appendix 2.S4).

The final model was fitted for the 162 countries with data: 135 with and 27 without threatened mammals. The latter group is formed by two distinct types of countries: 15 small islands included in the group of *Small Islands Developing States* (SIDS, as defined at the UNCED 1992) and 12 European countries (including island-countries Malta and Iceland). The countries with at least one threatened mammal form a more heterogeneous group, which we describe in the next section. The final model provided a good fit to the data, explaining 61.9% of the deviance, with 37.4% explained by the control variables (country land area, total mammalian richness and shared mammals) and 24.5% associated to the four socioeconomic variables identified as relevant. This final model also had high sensitivity (0.964, power to identify positives) and specificity (0.818, power to identify negatives); and excellent overall predictive ability (AUC= 0.968).

Abundance of threatened species

Socioeconomic indicators also correlate with threatened mammal abundance at the country level. International tourism (receipts) and life expectancy indicators follow an

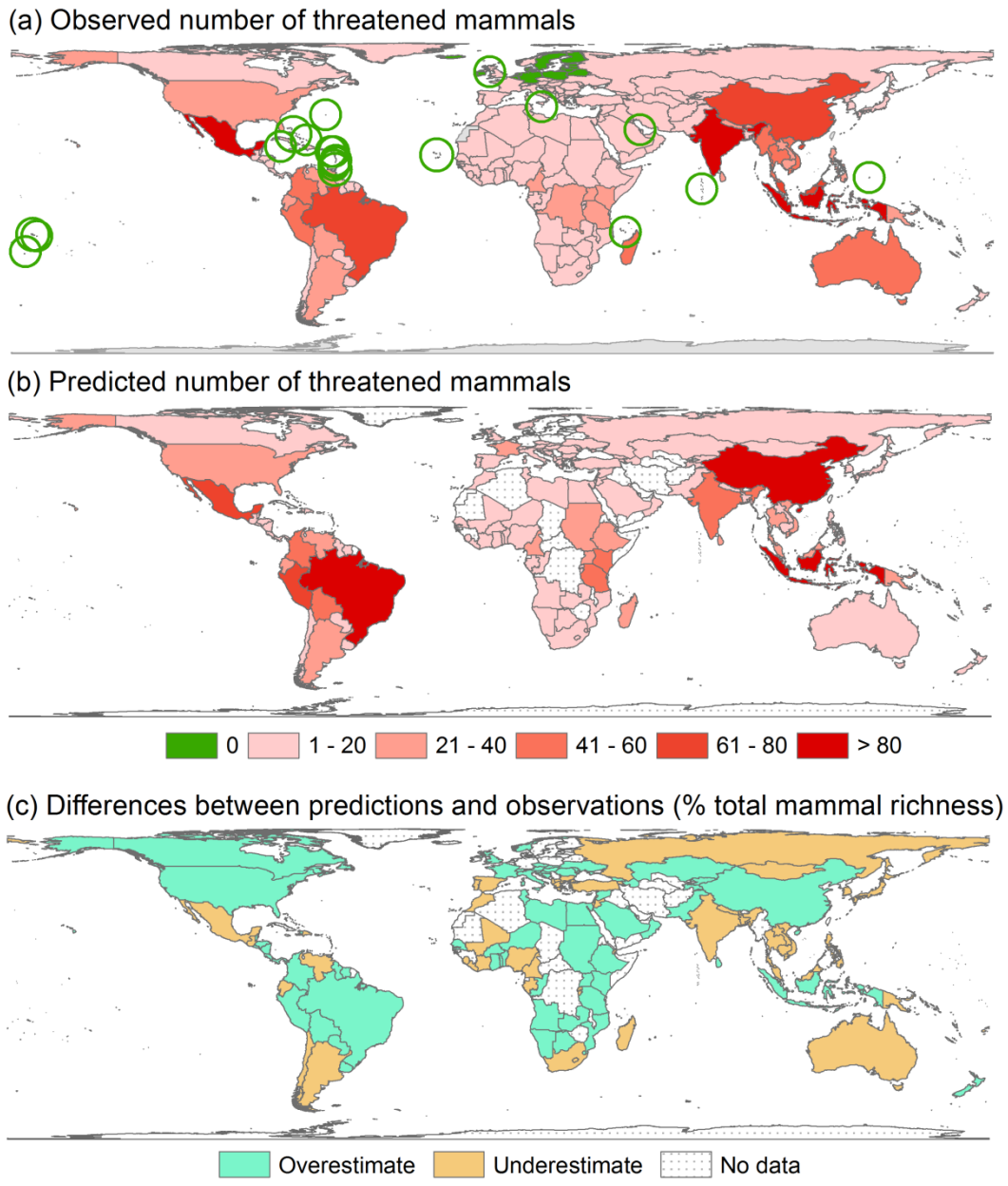

Figure 2.2. Observed (A) and predicted (B) number of threatened mammal species per country. (C) represents the differences between predicted and observed values divided by the total mammalian richness of the country. Both overestimated and underestimated values are within the ±0.14% range; excepting Cyprus, Indonesia, Barbados, Seychelles, New Zealand and Mauritius that present overestimates > 0.14%. *No data* indicates that selected socioeconomic indicators were not available for those countries.

Table 2.1. Results of the final model exploring the association of socioeconomic indicators and the probability of presence of threatened mammals by country (Data Deficient species considered as non-threatened. N=162). We report the best coefficient estimate and its standard error [β (SE)] and the mean odds ratio (OR) with the 95 % confidence interval (CI) for all variables included in the final model.

Variables	β (SE)	OR (95 %CI)
Socioeconomic		
Urban population[2]	-0.00 (0.001)·	1.00 (0.997;1.000)
Urban population	0.20 (0.106)·	1.22 (1.008;1.538)
Population growth	1.85 (0.566)**	6.33 (2.282;21.828)
Arable land[2]	0.00 (0.002)*	1.00 (1.001;1.008)
Arable land	-0.20 (0.085)*	0.82 (0.683;0.960)
Tourism receipts[2]	-0.01 (0.002)**	0.99 (0.991;0.998)
Tourism receipts	0.39 (0.140)**	1.47 (1.166;2.034)
Control		
Total mammals	0.130 (0.034)***	1.13 (1.072;1.226)
Land area	0.000 (0.002)	1.00 (1.000;1.000)
Shared mammals	-0.710 (1.559)	0.49 (0.021;9.840)

[2] quadratic term; ***P <0.001, **P<0.01, *P<0.05, · P< 0.1

inverted-U relationship with the total number of threatened mammals by country, whereas the rest of selected variables linearly correlate with the response variable. In particular, the final model shows that countries with more threatened mammals have lower percentages of urban population, intermediate to high life expectancies, generate fewer imports but more exports of goods and services, and their share in exports due to expenditures by international inbound visitors (international tourism receipts) are low to intermediate (Table 2.2; Fig. 2.4). This final model highlights the importance of transborder impacts and included data from 125 countries that have between 1 and 177 threatened mammals (the full range of observed values in the World. Table 2.S3), and explained 79.8% of the deviance, 72.0% corresponding to the control variables and 7.8% to the selected socioeconomic indicators. Model predictions for each country were generally accurate with only small errors in prediction representing ±0.14% of the total mammalian richness of the country. Only six countries were predicted to have considerably more threatened mammals (>0.14%)

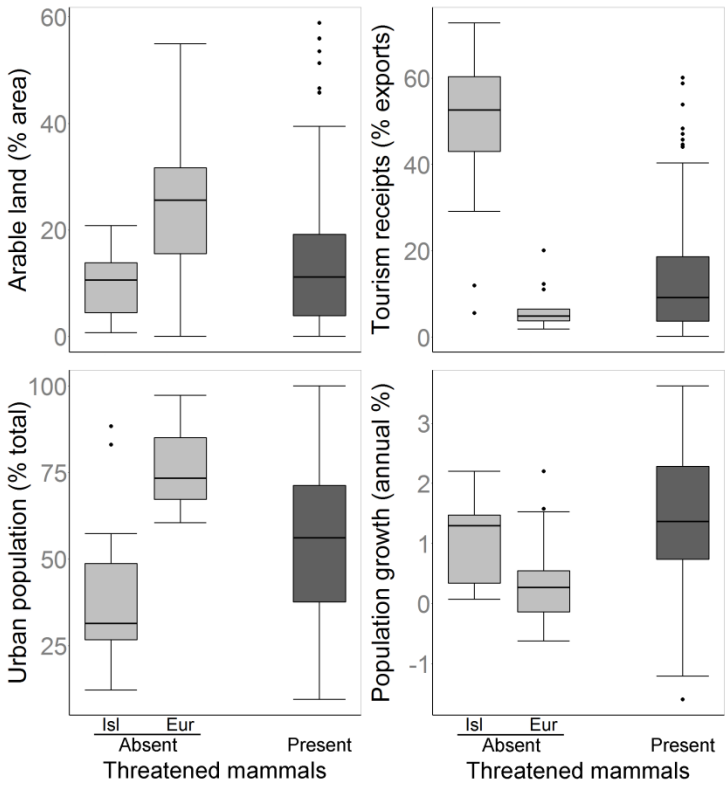

Figure 2.3. Observed values for the key socioeconomic variables associated with differences in the probability of presence of threatened mammals for countries with threatened mammals (dark grey bars; *present*) and countries without threatened mammals (light grey bars; *absent*). *Isl*, subgroup of SIDS; *Eur*, subgroup of European countries.

Table 2.2. Results of the final model exploring the association between socioeconomic indicators and the abundance of threatened mammals by country. (Data Deficient species considered as non-threatened. N=125). We report the best coefficient estimate and its standard error [β (SE)] for all variables included in the final model.

Variables	β (SE)
Socioeconomic	
Urban population	-0.01 (0.003)***
Imports GS	-0.01 (0.004)**
Exports GS	0.01 (0.004)**
Life expectancy[2]	-0.00 (0.001)*
Life expectancy	0.17 (0.067)*
Tourism receipts[2]	-0.00 (0.031)**
Tourism receipts	0.03 (0.014)*
Control	
Total mammals	0.01 (0.000)***
Land area	0.00 (0.000)
Shared mammals	-0.92 (0.191)***

[2] quadratic term; ***P<0.001, **P<0.01, *P<0.05, ·P< 0.1

than those currently listed: Cyprus, Indonesia, Barbados, Seychelles, New Zealand and Mauritius (Fig. 2.2 b and c). Results were qualitatively the same when DD species were classified as threatened although the final model included three additional indicators: annual population growth (%), CO_2 emissions and international expenditures on tourism (% imports. Appendix 2.S4).

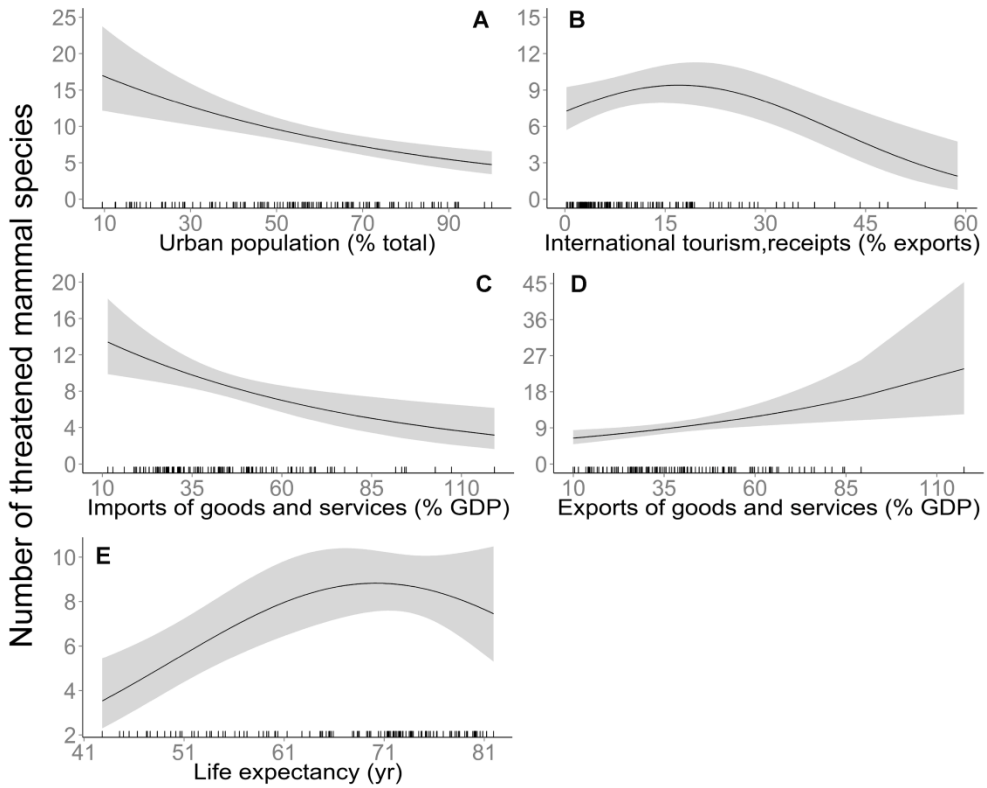

Figure 2.4. Predicted relationships between key socioeconomic variables and the abundance of threatened mammals by country (DD species classified as non-threatened). Model predictions were based on the final model (Table 2.2) and estimated by exploring the range of observed values for each indicator while using the median observed value for other variables in the model (Median values: total mammalian richness = 130; land area = 196,800 sq·km; shared mammals = 0.7646; urban population = 56.20%; international tourism, receipts = 8.56%; imports of goods and services = 42.64%; exports of goods and services =36.45%; life expectancy = 71.38). Shadowed area represents the confidence intervals (95%). Singapur was removed from graphs C and D to facilitate visualization. Singapur has extremely high values for these two indicators (imports of goods and services (% GDP)= 200.452; exports of goods and services (% GDP)= 228.007). The distribution of the observed data for each indicator is indicated over the x-axis by small bars.

All fitted models (Tables 2.1, 2.2) —evaluating presence and abundance of threatened mammals— include three control variables (total mammalian richness, country land surface and shared mammals). As expected, the presence and abundance of threatened mammals is always positively associated with total mammalian richness. Once richness is taken into account, the total land area does not significantly influence the presence and abundance of threatened mammals. The percentage of shared mammals has no significant effect on the probability of presence of threatened species, but in the abundance model countries with more shared species tend to have fewer threatened mammals.

Discussion

Our results show that both presence and abundance of threatened mammalian species correlate with particular socioeconomic features at a global scale (Appendix 2.S5 provides maps representing the observed values per country for all indicators identified as relevant). While our analyses do not evaluate how these socioeconomic conditions associate with the actual processes and threats that affect mammals, our results offer interesting follow-up questions and hypotheses regarding those aspects of socioeconomic development which could be more influential for mammalian conservation.

Interestingly, our results show two clearly distinct types of countries that lack threatened mammals: SIDS (*Small Islands Developing States*) and well-developed and relatively small European countries. SIDS have suffered relatively minor changes in land use judging by their low levels of arable land and urban population, but tourism constitutes an important part of their economies (Fig. 2.3) and also a potential threat to their biodiversity (Gössling et al. 2002; McElroy 2003). Although SIDS are characterized by economic and environmental vulnerability (Kier et al. 2009; Teelucksingh & Watson 2013), these small islands have generally low mammalian richness due to their small size and isolation (Whittaker & Fernández-Palacios 2007), thus limiting the number of potential mammals that could be at risk. Small European countries, on the other hand, have higher percentages of arable land and urban

population, the result of a history of land transformation that is not reflected in the amount of mammals currently at risk at this scale (Falcucci et al. 2007; Mortelliti et al. 2010). For both groups of countries, the recent record of extinct species (post 15th century) does not seem to explain the absence of threatened species. The amount of extinct and extinct in the wild species reported by the IUCN within these countries is four species in four SIDS (one on each), and one in one European country (Table 2.S7), no more than the number of extinct species in other areas. An alternative explanation for the lack of threatened species in these countries could be that their most vulnerable –and probably scarce– mammals became extinct long ago and/or that currently extant species have been extirpated (are locally extinct) from these territories (Ceballos & Ehrlich 2002; Morrison et al. 2007). Additionally, some of these countries have nowadays the resources and will to implement conservation policies to protect their remaining fauna which could reduce the number of species listed as threatened (Pullin et al. 2009). Although a priori we could expect that the lack of threatened mammals would be associated with the "most pristine" or "less humanized" countries, our results do not reflect that trend. By exploring for the first time the socioeconomic profiles of countries harboring no threatened mammals our study offers new, testable, hypotheses to explain these absences including the effects of increased conservation actions, local extirpations and ancient global extinctions.

Among countries with one or more threatened mammals, we identified diverse indicators, with both linear and quadratic relationships, as associated with the number of threatened mammals (Fig. 2.4). All else being equal, states with a higher proportion of rural population appear to be associated with higher numbers of threatened species, which suggests that more threats could be associated with rural development than with predominantly urban countries. Future research would be necessary to explore this association, but threats associated with nations with higher proportions of rural population are probably related to land transformation for agriculture and the resulting habitat loss for many mammals, as well as side effects of land use intensity such as pollution and exotic species introductions (Laurance et al. 2014). In addition, more urbanized countries could have already lost many of their most vulnerable species and thus could present apparently better conservation status. We found that

human life expectancy, an indicator of overall socioeconomic development, is also associated with mammalian conservation status; with intermediate to high life expectancies being associated with more threatened species. This non-linear relationship often described as an environmental Kuznets curve was also reported in a previous study that used another aggregated indicator, per capita income by country, which is highly correlated with life expectancy (Mcpherson & Nieswiadomy 2005). Finally, an interesting result from our analyses is the identified importance of trade and flux of services, goods and people among countries (Fig. 2.4), all of them linked to the fast globalization process we are witnessing.

Recent studies suggest that international trade is associated with 30% of global species threats (Lenzen et al. 2012) and some authors have equated the imports of certain goods to the exports of ecological impacts (Meyfroidt et al. 2010). While our results support these ideas, further research would be necessary to assess the actual impacts caused by this trade including conversion of land to exportable key crops (e.g., coffee, soybean, oils, etc), logging, and overhunting for pet trade (Lenzen et al. 2012). In the meantime, given the apparent importance of trade, we propose that land use classifications and assessments of threats should explicitly consider international trade, for example separating land use changes associated with internal production from those destined to exports. In addition to the importance of trade of goods and services we found that international tourism (visiting) is also correlated with the number of threatened mammals but with a perhaps unexpected pattern. Apparently, countries whose economies highly depend on international tourism have fewer threatened mammals than those with intermediate levels. Within this group we can find many SIDS (e.g., Netherlands Antilles, Barbados) which have high levels of tourism but, as explained above, are areas naturally poor in mammals.

By considering a diversity of indicators we also show that neither of the two proposed general hypotheses linking biodiversity and socioeconomic development is consistently supported as both linear and quadratic relationships are observed (Fig. 2.4). For some indicators our results suggest that the effect of development on biodiversity is non-linear supporting the hypothesis that fewer threatened mammals in more developed countries can be a consequence of the increasing environmental

concern and stricter environmental regulations that often accompany socioeconomic development. In other cases, the relationships are linear with more development associated with more threatened species and no subsequent improvement. This diversity of association patterns highlight why using a single development indicator is not advisable (Moran et al. 2008; Nielsen 2011), and also advocates for considering non-linear relationships when testing the relationship between socio-economic development and environmental impact.

Our results also deliver a useful message for conservation planning highlighting countries where the observed number of threatened mammals is smaller or greater than expected by their socioeconomic profile. For example countries such as Brazil or United States (countries in green in Fig. 2.2c) have fewer threatened mammals than predicted perhaps because they have a mechanism that is acting to decrease threats to mammals (such as effective conservation measures), and/or because they are areas naturally occupied by less susceptible species (e.g., more cosmopolitan/resilient mammals). Conversely, countries such as India or Australia (countries in brown in Fig. 2.2c) harbor more threatened mammals than predicted by their socioeconomic characteristics. In these countries human threats may be especially intense and fast changing (not yet be accounted for in available assessments) and/or mammals occupying these regions are particularly sensitive (e.g., endemic or intrinsically vulnerable). Future studies that aim to disentangle the role that these mechanisms play at finer scales are important and would be useful to complement previous global prioritization scenarios (Eklund et al. 2011; Visconti et al. 2011).

Finally, we would like to discuss some limitations of our study. First, we could not explore causal relationships or establish which specific human actions associated with socioeconomic development are directly responsible for the increased vulnerability. Nevertheless, our results lead to interesting follow-up questions such as: What are the threats and processes that occur in rural countries that lead to increase mammalian vulnerability? What are the specific activities related to the exports of goods and services that are so damaging for mammals? What underlying factors make countries with high levels of international tourism less likely to contain threatened

mammals? Although we do not know the answers, and often lack the data to explore the questions, our study provides guidance on key issues that need to be addressed. Second, our analyses are based on countries that comprise widely different areas (2–16,380,000 km^2) that may not be well-represented by average values of direct descriptors of land use or environmental characteristics. This could be the reason why our final models do not include indicators, other than % arable land, more directly linked to local land use changes. Lotz & Allen (2013) conducted a similar country-level study of vulnerability to socioeconomic factors and identified some land use variables as relevant, including agricultural intensity and surface of protected area. Our results likely differ from those of Lotz & Allen (2013) due to methodological differences: we use a hierarchical model building approach to maximize data use, tested both linear and quadratic relationships, and analyzed countries with and without threatened species separately. In addition, Lotz & Allen (2013) evaluated a different subset of indicators using a different subset of socioeconomic indicators and also including variables that summarized ecological features of analyzed countries, highlighting the importance of careful variable selection and hypotheses driven analyses. Finally, we would like to note that the lack of socioeconomic information for some countries is likely limiting our full understanding of reality, as analyses may exclude potentially key factors for which information is simply not currently available.

In conclusion, our results provide a global comprehensive characterization of the socioeconomic profiles of countries with more (and less) threatened mammalian fauna. Future work would be necessary to identify the specific human actions that cause increased number of threatened species and thus, to provide direct management recommendations. It would also be enlightening to explore the historical processes that have triggered current conservation status. Some of those countries lacking threatened mammals may actually have lost their most vulnerable species and now appear as better preserved areas. Conversely, some of the countries with many threatened species could in fact be acting as refuges for species that were originally more widespread and now can only persist in these areas. Meanwhile, these profiles can help us identify human development issues that may be particularly worrisome but are not yet well-recognized. For example, our analyses emphasize the role of

globalization for mammalian conservation status. Our attention is often focused on human activities occurring at the same site as the environmental damage, while we forget that in today's globalized world, drivers located far away may be responsible for many of the observed changes. Many developed countries have a relatively well-protected fauna; however, the impact of their activities and policies extends to other countries. The effect of transborder impacts has only been explicitly addressed recently (Meyfroidt et al. 2010; Lenzen et al. 2012), yet these impacts likely play an important role in conservation.

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Supporting Information

Appendix 2.S1. Definition and description of biodiversity conservation status estimates, and socioeconomic indicators used in the analyses.

Table 2.S1. Correspondence between categories (topics) used by the World Bank to classify socioeconomic indicators and the simplified categories used for this study.

Topic (World Bank classification)	Category
Environment: Land use Environment: Agricultural production	Agriculture
Economic Policy & Debt: National accounts: Growth rates Economic Policy & Debt: National accounts: US$ at constant 2000 prices: Aggregate indicators Economic Policy & Debt: Purchasing power parity Economic Policy & Debt: National accounts: Shares of GDP & other Economic Policy & Debt: National accounts: Adjusted savings & income Poverty: Poverty rates Poverty: Income distribution Poverty: Poverty rates	Economy
Education: Inputs Education: Outcomes	Education
Environment: Land use Environment: Biodiversity & protected areas Environment: Emissions Environment: Natural resources contribution to GDP Environment: Energy production & use Environment: Water pollution Environment: Freshwater	Environment
Health: Mortality Health: Reproductive health Health: Health services Health: Disease prevention	Health
Infrastructure: Technology Infrastructure: Transportation	Infrastructure
Labor & Social Protection: Migration Labor & Social Protection: Labor force structure Labor & Social Protection: Economic activity	Labor and social protection
Health: Population: Structure Health: Population: Dynamics Environment: Density & urbanization	Population
Private Sector & Trade: Exports Private Sector & Trade: Travel & tourism	Private sector

Table 2.S2. List of socioeconomic indicators hypothesized to have an influence on the presence and abundance of threatened mammals by country (grouped by the categories described in Table 2.S1). *%:* shows the percentage of countries with data for that indicator (2005). Reasons for excluding variables from the analyses were insufficiency of data (*Ins*; <70% countries with information for that variable) or high correlation with other indicators (*Corr*; Spearman $\rho > |0.8|$). The rest of variables (-) were included in the models by category.

Indicator	**%**	**Reason for exclusion**
Agriculture		
Agricultural land (% of land area)	98	-
Arable land (% of land area)	98	-
Fertilizer consumption (kilograms per hectare of arable land)	73	-
Agricultural irrigated land (% of total agricultural land)	28	Ins.
Economy		
GDP per capita growth (annual %)	93	-
GDP per capita, PPP (constant 2005 international $)	87	-
Agriculture, value added (% of GDP)	83	Corr. with *GDP per capita*
Imports of goods and services (% of GDP)	86	-
Exports of goods and services (% of GDP)	86	-
GINI index	19	Ins.
Poverty gap at $2 a day (PPP) (%)	20	Ins.
Poverty gap at national poverty line (%)	10	Ins.
Education		
Literacy rate, adult total (% of people ages 15 and above)	8	Ins.
Public spending on education, total (% of GDP)	50	Ins.
Research and development expenditure (% of GDP)	41	Ins.
Environment		
CO_2 emissions (metric tons per capita)	94	-
Forest area (% of land area)	100	-
Mineral rents (% of GDP)	88	-
Terrestrial protected areas (% of total land area)	98	-
Total natural resources rents (% GDP)	93	-
Organic water pollutant (BOD) emissions (kg per day)	34	Ins.
Health		
Birth rate, crude (per 1,000 people)	96	Corr. with *Improved sanitation facilities, Fertility rate* and *Life expectancy*
Fertility rate, total (births per woman)	94	-
Health expenditure per capita, PPP (constant 2005 international $)	90	Corr. with *Improved sanitation facilities* and *Life expectancy*
Improved sanitation facilities (% of population with access)	86	Corr. with *Life expectancy* and *Birth rate*
Life expectancy at birth, total (years)	95	-

Indicator	%	Reason for exclusion
Infrastructures		
Road density (km of road per 100 sq. km of land area)	38	Ins.
Labor and social protection		
Labor participation rate, female (% of female population ages 15+)	90	-
Net migration	94	-
Population		
Population density (habitant/sq·km)	100	-
Population, total	100	Corr. with *Land area*
Population growth (annual %)	99	-
Rural population (% of total population)	100	Corr. with *Urban population*
Rural population growth (annual %)	97	-
Urban population (% of total population)	100	-
Urban population growth (annual %)	99	Corr. with *Population growth*
Private sector		
Merchandise exports to high-income economies (% of total merchandise exports)	89	-
International tourism, expenditures (% of total imports)	79	-
International tourism, receipts (% of total exports)	79	-

Table 2.S3. Descriptive statistics of all variables used in the analyses grouped by modeling categories.

Name	Units	N	Median	(min - max)
Response variable				
Abundance of threatened mammals	number of species	204	5.000	(0.000-177.000)
Control				
Land area	1000 sq. km	204	103.700	(0.002-16380.000)
Mean shared mammals with neighboring countries	% of total richness of mammals	204	0.728	(0.000-1.000)
Total richness of mammmals	number of species	204	79.000	(1.000-649.000)
Agriculture				
Agricultural land	% of land area	200	38.420	(0.473-89.020)
Arable land	% of land area	199	10.720	(0.043-58.870)
Fertilizer consumption	kilograms per hectare of arable land	148	69.720	(0.000-2719.000)
Economy				
Imports of goods and services	% of GDP	176	44.020	(11.520-200.450)
Exports of goods and services	% of GDP	176	39.000	(5.782-228.007)

Name	Units	N	Median	(min - max)
GDP per capita growth	annual %	189	3.142	(-5.989-25.113)
GDP per capita, PPP	constant 2005 international $	177	6200.200	(265.900-68319.200)
Environment				
CO_2 emissions	metric tons per capita	191	2.288	(0.022-64.119)
Forest area	% of land area	204	30.620	(0.000-94.720)
Mineral rents	% of GDP	180	0.000	(0.000-27.939)
Terrestrial protected areas	% of total land area	199	9.448	(0.000-53.750)
Total natural resources rents	% of GDP	189	1.951	(0.000-206.507)
Health				
Fertility rate, total	births per woman	192	2.432	(1.080-7.267)
Life expectancy at birth, total	years	193	71.360	(41.470-81.980)
Labor and social protection				
Labor participation rate, total	% of total population ages 15+	180	63.850	(37.300-89.400)
Net migration	1000 people	187	-3.000	(-2702.060-5675.799)
Population				
Population density	habitant/sq·km	204	74.328	(0.139-16226.500)
Population growth	annual %	202	1.337	(-1.591-10.518)
Rural population growth	annual %	197	0.459	(-21.880-8.516)
Urban population	% of total	203	57.400	(9.500-100.000)
Private sector				
International tourism, expenditures	% of total imports	162	5.462	(0.226-21.024)
International tourism, receipts	% of total exports	162	9.211	(0.232-72.774)
Merchandise exports to high-income economies	% of total merchandise exports	181	71.655	(5.524-124.836)

Table 2.S4. Definitions and sources of the variables considered for analyses grouped by modeling categories, including those excluded due to their high correlation with other indicators (see Table 2.S2). All data can be accessed on <http://data.worldbank.org/>. For socioeconomic variables we provide the World's Bank definition.

Name	Definition	Source
Response variable		
Abundance of threatened mammals	Total number of mammals included in the categories critically endangered (CR), endangered (EN) and vulnerable (VU).	The IUCN Red List of Threatened Species (Version 3, IUCN 2012)
Control		

Name	Definition	Source
Land area	Land area is a country's total area, excluding area under inland water bodies, national claims to continental shelf, and exclusive economic zones. In most cases the definition of inland water bodies includes major rivers and lakes.	Food and Agriculture Organization, electronic files and web site.
Mean shared mammals with neighboring countries	Mean number of mammals shared with bordering countries (sharing at least one border point), divided by total richness of mammals distributed within the country	Own calculations (derived from the maps of The IUCN Red List of Threatened Species (Version 3, IUCN 2012))
Total richness of mammmals	Total number of mammals whose distribution is included within the border of a country, either partially or totally	Maps of The IUCN Red List of Threatened Species (Version 3, IUCN 2012)
Agriculture		
Agricultural land	Agricultural land refers to the share of land area that is arable, under permanent crops, and under permanent pastures. Arable land includes land defined by the FAO as land under temporary crops (double-cropped areas are counted once), temporary meadows for mowing or for pasture, land under market or kitchen gardens, and land temporarily fallow. Land abandoned as a result of shifting cultivation is excluded. Land under permanent crops is land cultivated with crops that occupy the land for long periods and need not be replanted after each harvest, such as cocoa, coffee, and rubber. This category includes land under flowering shrubs, fruit trees, nut trees, and vines, but excludes land under trees grown for wood or timber. Permanent pasture is land used for five or more years for forage, including natural and cultivated crops.	Food and Agriculture Organization, electronic files and web site.
Arable land	Arable land includes land defined by the FAO as land under temporary crops (double-cropped areas are counted once), temporary meadows for mowing or for pasture, land under market or kitchen gardens, and land temporarily fallow. Land abandoned as a result of shifting cultivation is excluded.	Food and Agriculture Organization, electronic files and web site.

Name	Definition	Source
Fertilizer consumption	Fertilizer consumption (100 grams per hectare of arable land) measures the quantity of plant nutrients used per unit of arable land. Fertilizer products cover nitrogenous, potash, and phosphate fertilizers (including ground rock phosphate). Traditional nutrients--animal and plant manures--are not included. For the purpose of data dissemination, FAO has adopted the concept of a calendar year (January to December). Some countries compile fertilizer data on a calendar year basis, while others are on a split-year basis. Arable land includes land defined by the FAO as land under temporary crops (double-cropped areas are counted once), temporary meadows for mowing or for pasture, land under market or kitchen gardens, and land temporarily fallow. Land abandoned as a result of shifting cultivation is excluded.	Food and Agriculture Organization, electronic files and web site.
Economy		
Agriculture, value added[1]	Agriculture corresponds to ISIC divisions 1-5 and includes forestry, hunting, and fishing, as well as cultivation of crops and livestock production. Value added is the net output of a sector after adding up all outputs and subtracting intermediate inputs. It is calculated without making deductions for depreciation of fabricated assets or depletion and degradation of natural resources. The origin of value added is determined by the International Standard Industrial Classification (ISIC), revision 3. Note: For VAB countries, gross value added at factor cost is used as the denominator.	World Bank national accounts data, and OECD National Accounts data files.
Imports of goods and services	Imports of goods and services represent the value of all goods and other market services received from the rest of the world. They include the value of merchandise, freight, insurance, transport, travel, royalties, license fees, and other services, such as communication, construction, financial, information, business, personal, and government services. They exclude compensation of employees and investment income (formerly called factor services) and transfer payments.	World Bank national accounts data, and OECD National Accounts data files.

Name	Definition	Source
Exports of goods and services	Exports of goods and services represent the value of all goods and other market services provided to the rest of the world. They include the value of merchandise, freight, insurance, transport, travel, royalties, license fees, and other services, such as communication, construction, financial, information, business, personal, and government services. They exclude compensation of employees and investment income (formerly called factor services) and transfer payments.	World Bank national accounts data, and OECD National Accounts data files.
GDP per capita growth	Annual percentage growth rate of GDP per capita based on constant local currency. GDP per capita is gross domestic product divided by midyear population. GDP at purchaser's prices is the sum of gross value added by all resident producers in the economy plus any product taxes and minus any subsidies not included in the value of the products. It is calculated without making deductions for depreciation of fabricated assets or for depletion and degradation of natural resources.	World Bank national accounts data, and OECD National Accounts data files.
GDP per capita, PPP	GDP per capita based on purchasing power parity (PPP). PPP GDP is gross domestic product converted to international dollars using purchasing power parity rates. An international dollar has the same purchasing power over GDP as the U.S. dollar has in the United States. GDP at purchaser's prices is the sum of gross value added by all resident producers in the economy plus any product taxes and minus any subsidies not included in the value of the products. It is calculated without making deductions for depreciation of fabricated assets or for depletion and degradation of natural resources. Data are in constant 2005 international dollars.	World Bank, International Comparison Program database.
Environment		
CO_2 emissions	Carbon dioxide emissions are those stemming from the burning of fossil fuels and the manufacture of cement. They include carbon dioxide produced during consumption of solid, liquid, and gas fuels and gas flaring.	Carbon Dioxide Information Analysis Center, Environmental Sciences Division, Oak Ridge National Laboratory, Tennessee, United States.
Forest area	Forest area is land under natural or planted stands of trees of at least 5 meters in situ, whether productive or not, and excludes tree stands in agricultural production systems (for example, in fruit plantations and agroforestry systems) and trees in urban parks and gardens.	Food and Agriculture Organization, electronic files and web site.

Name	Definition	Source
Mineral rents	Mineral rents are the difference between the value of production for a stock of minerals at world prices and their total costs of production. Minerals included in the calculation are tin, gold, lead, zinc, iron, copper, nickel, silver, bauxite, and phosphate.	Estimates based on sources and methods described in "The Changing Wealth of Nations: Measuring Sustainable Development in the New Millennium" (World Bank, 2011).
Terrestrial protected areas	Terrestrial protected areas are those officially documented by national authorities.	United Nations Environmental Program and the World Conservation Monitoring Centre, as compiled by the World Resources Institute, based on data from national authorities, national legislation and international agreements.
Total natural resources rents	Total natural resources rents are the sum of oil rents, natural gas rents, coal rents (hard and soft), mineral rents, and forest rents.	Estimates based on sources and methods described in "The Changing Wealth of Nations: Measuring Sustainable Development in the New Millennium" (World Bank, 2011).
Health		
Birth rate, crude[†]	Crude birth rate indicates the number of live births occurring during the year, per 1,000 population estimated at midyear. Subtracting the crude death rate from the crude birth rate provides the rate of natural increase, which is equal to the rate of population change in the absence of migration.	(1) United Nations Population Division. 2009. World Population Prospects: The 2008 Revision. New York, United Nations, Department of Economic and Social Affairs (advanced Excel tables), (2) United Nations Statistical Division. Population and Vital Statistics Report (various years), (3) Census reports and other statistical publications from national statistical offices, (4) Eurostat: Demographic Statistics, (5) Secretariat of the Pacific Community: Statistics and Demography Programme, and (6) U.S. Census Bureau: International Database.
Fertility rate, total	Total fertility rate represents the number of children that would be born to a woman if she were to live to the end of her childbearing years and bear children in accordance with current age-specific fertility rates.	(1) United Nations Population Division. 2009. World Population Prospects: The 2008 Revision. New York, United Nations, Department of Economic and Social Affairs (advanced Excel tables). Available at http://esa.un.org/unpd/wpp2008/index.htm. (2) Census reports and other statistical publications from national statistical offices, (3) Eurostat: Demographic Statistics, (4) Secretariat of the Pacific Community: Statistics and Demography Programme, (5) U.S. Census Bureau: International Database, and (6) household surveys conducted by national agencies, Macro International, and the U.S. Centers for Disease Control and Prevention.

Name	Definition	Source
Health expenditure per capita, PPP[†]	Total health expenditure is the sum of public and private health expenditures as a ratio of total population. It covers the provision of health services (preventive and curative), family planning activities, nutrition activities, and emergency aid designated for health but does not include provision of water and sanitation. Data are in international dollars converted using 2005 purchasing power parity (PPP) rates.	World Health Organization National Health Account database (www.who.int/nha/en) supplemented by country data.
Improved sanitation facilities[†]	Access to improved sanitation facilities refers to the percentage of the population with at least adequate access to excreta disposal facilities that can effectively prevent human, animal, and insect contact with excreta. Improved facilities range from simple but protected pit latrines to flush toilets with a sewerage connection. To be effective, facilities must be correctly constructed and properly maintained.	World Health Organization and United Nations Children's Fund, Joint Measurement Programme (JMP) (http://www.wssinfo.org/).
Life expectancy at birth, total	Life expectancy at birth indicates the number of years a newborn infant would live if prevailing patterns of mortality at the time of its birth were to stay the same throughout its life.	Derived from male and female life expectancy at birth. Male and female life expectancy source: (1) United Nations Population Division. 2009. World Population Prospects: The 2008 Revision. New York, United Nations, Department of Economic and Social Affairs (advanced Excel tables), (2) Census reports and other statistical publications from national statistical offices, (3) Eurostat: Demographic Statistics, (4) Secretariat of the Pacific Community: Statistics and Demography Programme, and (5) U.S. Census Bureau: International Database.
Labor and social protection		
Labor participation rate, total	Labor force participation rate is the proportion of the population ages 15 and older that is economically active: all people who supply labor for the production of goods and services during a specified period.	International Labour Organization, Key Indicators of the Labour Market database.

Name	Definition	Source
Net migration	Net migration is the net total of migrants during the period, that is, the total number of immigrants less the annual number of emigrants, including both citizens and noncitizens. Data are five-year estimates. To derive estimates of net migration, the United Nations Population Division takes into account the past migration history of a country or area, the migration policy of a country, and the influx of refugees in recent periods. The data to calculate these official estimates come from a variety of sources, including border statistics, administrative records, surveys, and censuses. When no official estimates can be made because of insufficient data, net migration is derived through the balance equation, which is the difference between overall population growth and the natural increase during the 1990-2000 intercensal period.	United Nations Population Division, World Population Prospects 2008.
Population		
Population density	Population density was calculated by dividing total population byt land area	Own calculations (derived from World Bank)
Population, total[†]	Total population is based on the de facto definition of population, which counts all residents regardless of legal status or citizenship--except for refugees not permanently settled in the country of asylum, who are generally considered part of the population of their country of origin. The values shown are midyear estimates.	(1) United Nations Population Division. 2009. World Population Prospects: The 2008 Revision. New York, United Nations, Department of Economic and Social Affairs (advanced Excel tables). Available at http://esa.un.org/unpd/wpp2008/index.htm. (2) Census reports and other statistical publications from national statistical offices, (3) Eurostat: Demographic Statistics, (4) Secretariat of the Pacific Community: Statistics and Demography Programme, (5) U.S. Census Bureau: International Database, and (6) World bank estimates based on the data from the sources above, household surveys conducted by national agencies, Macro International, the U.S. Centers for Disease Control and Prevention, and refugees statistics from the United Nations High Commissioner for Refugees.

Name	Definition	Source
Population growth	Annual population growth rate for year t is the exponential rate of growth of midyear population from year t-1 to t, expressed as a percentage . Population is based on the de facto definition of population, which counts all residents regardless of legal status or citizenship--except for refugees not permanently settled in the country of asylum, who are generally considered part of the population of the country of origin.	Derived from total population. Population source: (1) United Nations Population Division. 2009. World Population Prospects: The 2008 Revision. New York, United Nations, Department of Economic and Social Affairs (advanced Excel tables). Available at http://esa.un.org/unpd/wpp2008/index.htm. (2) Census reports and other statistical publications from national statistical offices, (3) Eurostat: Demographic Statistics, (4) Secretariat of the Pacific Community: Statistics and Demography Programme, (5) U.S. Census Bureau: International Database, and (6) World bank estimates based on the data from the sources above, household surveys conducted by national agencies, Macro International, the U.S. Centers for Disease Control and Prevention, and refugees statistics from the United Nations High Commissioner for Refugees.
Rural population†	Rural population refers to people living in rural areas as defined by national statistical offices. It is calculated as the difference between total population and urban population.	World Bank Staff estimates based on United Nations, World Urbanization Prospects.
Rural population growth	Rural population refers to people living in rural areas as defined by national statistical offices. It is calculated as the difference between total population and urban population.	World Bank Staff estimates based on United Nations, World Urbanization Prospects.
Urban population	Urban population refers to people living in urban areas as defined by national statistical offices. It is calculated using World Bank population estimates and urban ratios from the United Nations World Urbanization Prospects.	World Bank Staff estimates based on United Nations, World Urbanization Prospects.
Urban population growth†	Urban population refers to people living in urban areas as defined by national statistical offices. It is calculated using World Bank population estimates and urban ratios from the United Nations World Urbanization Prospects.	World Bank Staff estimates based on United Nations, World Urbanization Prospects.
Private sector		
International tourism, expenditures	International tourism expenditures are expenditures of international outbound visitors in other countries, including payments to foreign carriers for international transport. These expenditures may include those by residents traveling abroad as same-day visitors, except in cases where these are important enough to justify separate classification. For some countries they do not include expenditures for passenger transport items. Their share in imports is	World Tourism Organization, Yearbook of Tourism Statistics, Compendium of Tourism Statistics and data files, and IMF and World Bank imports estimates.

Name	Definition	Source
	calculated as a ratio to imports of goods and services, which comprise all transactions between residents of a country and the rest of the world involving a change of ownership from nonresidents to residents of general merchandise, goods sent for processing and repairs, nonmonetary gold, and services.	
International tourism, receipts	International tourism receipts are expenditures by international inbound visitors, including payments to national carriers for international transport. These receipts include any other prepayment made for goods or services received in the destination country. They also may include receipts from same-day visitors, except when these are important enough to justify separate classification. For some countries they do not include receipts for passenger transport items. Their share in exports is calculated as a ratio to exports of goods and services, which comprise all transactions between residents of a country and the rest of the world involving a change of ownership from residents to nonresidents of general merchandise, goods sent for processing and repairs, nonmonetary gold, and services.	World Tourism Organization, Yearbook of Tourism Statistics, Compendium of Tourism Statistics and data files, and IMF and World Bank exports estimates.
Merchandise exports to high-income economies	Merchandise exports to high-income economies are the sum of merchandise exports from the reporting economy to high-income economies according to the World Bank classification of economies as of July 1, 2009. Data are expressed as a percentage of total merchandise exports by the economy. Data are computed only if at least half of the economies in the partner country group had non-missing data.	World Bank staff estimates based data from International Monetary Fund's Direction of Trade database.

†*: variables excluded from the models due to their high correlation ($\rho > |0.8|$) with others in any category*

Appendix 2.S2. Number of threatened and non-threatened species per country, and degree of agreement between national and global Red Lists.

Table 2.S5. Comparison between numbers of threatened species according to National vs. Global Red List, in countries with National Red Lists. The number of threatened species was calculated as the mean between the count with and without including data deficient species. *TOTAL* shows the total number of species considered in each of the lists. *Coinciding* number (*n*) is the number of species considered as threatened in both lists. The coinciding percentage (*%)* is the number of coinciding threatened species over the total regionally threatened species.

	National Red List		**Global Red List**		***Coinciding***	
Country	Threatened	TOTAL	Threatened	TOTAL	n	(%)
Argentina	47.0	147	65.5	351	19.5	(0.4)
Bangladesh	13.0	50	22.0	146	2.5	(0.2)
Bhutan	11.5	29	29.0	154	3.5	(0.3)
Canada	22.0	43	3.0	140	1.0	(0.0)
Colombia	25.0	25	69.5	445	18.5	(0.7)
Estonia	1.0	12	0.0	47	0.0	(0.0)
Finland	3.0	8	0.0	49	0.0	(0.0)
France	9.5	76	24.0	305	2.5	(0.3)
United Kingdom	2.0	2	2.0	59	0.0	(0.0)
Croatia	8.5	27	3.5	79	1.5	(0.2)
India	59.5	213	90.0	352	28.5	(0.5)
Israel	43.5	71	7.0	81	5.5	(0.1)
Japan	10.5	16	16.5	93	5.0	(0.5)
Sri Lanka	55.0	119	21.0	82	22.0	(0.4)
Maldives	1.0	2	0.0	2	0.0	(0.0)
Mongolia	30.5	88	7.5	115	5.0	(0.2)
Norway	7.0	13	1.0	49	0.0	(0.0)
Nepal	20.0	89	27.0	176	5.0	(0.3)
New Zealand	4.0	6	2.0	3	1.0	(0.3)
Pakistan	11.0	82	14.0	161	2.5	(0.2)
Poland	9.5	17	0.0	67	0.0	(0.0)
Sweden	8.5	16	0.0	52	0.0	(0.0)
Venezuela	48.5	103	47.0	341	26.5	(0.5)
MEAN	**19.6**	**54.5**	**19.6**	**145.6**	**6.5**	**(0.2)**

Table 2.S6. Comparison between numbers of non-threatened species according to National vs. Global Red List, in countries with National Red Lists. The number of non-threatened species was calculated as the mean between the count with and without including data deficient species. *TOTAL* shows the total number of species considered in each of the lists. *Coinciding* number (*n*) is the number of species considered as non-threatened in both lists. The coinciding percentage (*%)* is the number of coinciding non-threatened species over the total regionally non-threatened species.

	National Red Lists		**Global Red List**		***Coinciding***	
Country	Non-threatened	TOTAL	Non-threatened	TOTAL	n	(%)
Argentina	100.0	147	285.5	351	87.5	(0.9)
Bangladesh	37.0	50	124.0	146	36.5	(1.0)
Bhutan	17.5	29	125.0	154	17.5	(1.0)
Canada	21.0	43	137.0	140	16.0	(0.8)
Colombia	0.0	25	375.5	445	0.0	NA
Estonia	11.0	12	47.0	47	11.0	(1.0)
Finland	5.0	8	49.0	49	5.0	(1.0)
France	66.5	76	281.0	305	64.0	(1.0)
United Kingdom	0.0	2	57.0	59	0.0	NA
Croatia	18.5	27	75.5	79	18.0	(1.0)
India	153.5	213	262.0	352	138.0	(0.9)
Israel	27.5	71	74.0	81	27.5	(1.0)
Japan	5.5	16	76.5	93	5.5	(1.0)
Sri Lanka	64.0	119	61.0	82	59.0	(0.9)
Maldives	1.0	2	2.0	2	1.0	(1.0)
Mongolia	57.5	88	107.5	115	57.0	(1.0)
Norway	6.0	13	48.0	49	6.0	(1.0)
Nepal	69.0	89	149.0	176	68.0	(1.0)
New Zealand	2.0	6	1.0	3	0.0	(0.0)
Pakistan	71.0	82	147.0	161	71.0	(1.0)
Poland	7.5	17	67.0	67	7.5	(1.0)
Sweden	7.5	16	52.0	52	7.5	(1.0)
Venezuela	54.5	103	294.0	341	49.0	(0.9)
MEAN	**34.9**	**54.5**	**126.0**	**145.6**	**32.7**	**(0.9)**

Appendix 2.S3. List and characteristics of countries considered in the analyses. Predictions are based on models considering DD species as non-threatened.

Table 2.S7. List of the 36 countries containing no threatened mammal species according to IUCN Red List criteria. (TOT*, total of mammalian species listed for that country by the IUCN;* DD*, data deficient;* CR*, critically endangered;* EN*, endangered;* VU*, vulnerable;* LC*, least concern;* NT*, near threatened;* Non-thr *(Non-threatened), addition of the species classified as least concerned and near threatened;* Prediction Prsc*, predicted probability of harboring threatened mammals provided by the fitted model. Bold values indicate probabilities higher than 0.5, meaning that the model predicted these countries to have threatened species. Dashes indicate lack of data for the variables included in the final fitted model. Extinct in the wild (EW) and extinct (EX) species are out of the analyses.* SIDS, *refers to countries classified as Small Island Developing States*).

Country	Code	TOT	DD	CR	EN	VU	LC	NT	EX	EW	Non-thr	Prediction	SIDS
												Prsc	
American Samoa	ASM	2	0	0	0	0	1	1	0	0	2	-	No
Antigua and Barbuda	ATG	8	0	0	0	0	8	0	0	0	8	0.19	Yes
Bahamas, The	BHS	6	0	0	0	0	5	1	0	0	6	0.21	Yes
Bahrain	BHR	7	0	0	0	0	6	1	0	0	7	**0.74**	No
Belarus	BLR	62	0	0	0	0	56	6	0	0	62	0.1	No
Belgium	BEL	49	0	0	0	0	45	4	0	0	49	0.05	No
Bermuda	BMU	1	0	0	0	0	1	0	0	0	1	-	No
Cape Verde	CPV	2	0	0	0	0	2	0	0	0	2	**0.8**	Yes
Cayman Islands	CYM	5	0	0	0	0	4	1	0	0	5	-	No
Denmark	DNK	40	0	0	0	0	36	4	0	0	40	**0.6**	No
Estonia	EST	47	0	0	0	0	45	2	0	0	47	0.48	No
Finland	FIN	49	0	0	0	0	48	1	0	0	49	0.39	No
Germany	DEU	61	0	0	0	0	56	5	0	0	61	0.34	No
Grenada	GRD	13	2	0	0	0	11	0	0	0	11	0.44	Yes
Iceland	ISL	3	0	0	0	0	3	0	0	0	3	0.37	No
Ireland	IRL	21	0	0	0	0	19	2	0	0	21	0.22	No
Isle of Man	IMY	7	0	0	0	0	7	0	0	0	7	-	No
Latvia	LVA	49	0	0	0	0	46	3	0	0	49	0.1	No
Liechtenstein	LIE	56	0	0	0	0	52	4	0	0	56	-	No
Lithuania	LTU	49	0	0	0	0	45	4	0	0	49	0.1	No
Luxembourg	LUX	48	0	0	0	0	44	4	0	0	48	**0.73**	No
Maldives	MDV	2	0	0	0	0	2	0	0	0	2	0.12	Yes
Malta	MLT	8	0	0	0	0	7	1	0	0	8	0.07	No
Mayotte	MYT	1	0	0	0	0	1	0	0	0	1	-	No
Netherlands	NLD	46	0	0	0	0	42	4	0	0	46	0.11	No

Country	Code	TOT	DD	CR	EN	VU	LC	NT	EX	EW	Non-thr	Prediction	SIDS
												Prsc	
Palau	PLW	1	0	0	0	0	0	1	1	0	1	-	Yes
Poland	POL	67	0	0	0	0	59	8	1	0	67	**0.85**	No
Samoa	WSM	2	0	0	0	0	1	1	0	0	2	0	Yes
San Marino	SMR	48	1	0	0	0	41	6	0	0	47	-	No
St. Kitts and Nevis	KNA	7	0	0	0	0	7	0	1	0	7	**0.69**	Yes
St. Lucia	LCA	8	0	0	0	0	8	0	1	0	8	0.01	Yes
St. Vincent and the Grenadines	VCT	12	1	0	0	0	11	0	1	0	11	0.33	Yes
Sweden	SWE	52	0	0	0	0	48	4	0	0	52	0.46	No
Tonga	TON	1	0	0	0	0	1	0	0	0	1	0.04	Yes
Trinidad and Tobago	TTO	65	4	0	0	0	60	1	0	0	61	0.32	Yes
Turks and Caicos Islands	TCA	3	0	0	0	0	3	0	0	0	3	-	No

Table 2.S8. List of the 168 countries containing threatened mammal species according to IUCN Red List criteria. (TOT.*, total of species listed for that country by the IUCN;* DD*, data deficient;* CR*, critically endangered;* EN*, endangered;* VU*, vulnerable;* LC*, least concern;* NT*, near threatened;* Thr*.* (Threatened)*, addition of the species classified as vulnerable, endangered and critically endangered;* Non-thr. (Non-threatened)*, addition of the species classified as least concerned and near threatened;* Prediction Prs. (prediction of presence), *predicted probability of harboring threatened mammals provided by the fitted model. Bold values indicate probabilities lower than 0.5, meaning that these countries are predicted to have no threatened species.* Prediction Abd. (prediction of abundance), *predicted abundance of threateaned mammals according to the fitted model.* a, *Arrows indicate if the abundance model overestimates* (↑) *or underestimates* (↓)*. Dashes indicate lack of data for the variables included in the final fitted model. Extinct in the wild (EW) and extinct (EX) species are out of the analyses.* SIDS, *refers to countries classified as Small Island Developing States*).

Country	Code	TOT	DD	CR	EN	VU	LC	NT	EX	EW	Thr.	Non-thr	Prediction			SIDS
													Prs	Abd	a	
Afghanistan	AFG	115	5	0	2	4	97	7	0	0	6	104	-	-		No
Albania	ALB	71	3	0	0	3	60	5	0	0	3	65	1.0	2.1	↓	No
Algeria	DZA	78	1	1	4	5	59	8	0	1	10	67	-	-		No
Andorra	ADO	58	0	0	0	3	49	6	0	0	3	55	-	-		No
Angola	AGO	299	16	2	2	5	262	12	0	0	9	274	1.0	16.6	↑	No
Argentina	ARG	351	63	7	12	15	223	31	1	0	34	254	1.0	29.6	↓	No
Armenia	ARM	79	3	1	2	2	62	9	0	0	5	71	1.0	5.0	↓	No
Aruba	ABW	3	1	0	0	1	1	0	0	0	1	1	0.8	-		Yes
Australia	AUS	270	11	7	15	22	185	30	19	0	44	215	1.0	19.7	↓	No
Austria	AUT	72	2	1	0	1	63	5	0	0	2	68	1.0	5.3	↑	No

Country	Code	TOT	DD	CR	EN	VU	LC	NT	EX	EW	Thr.	Non-thr	Prediction		SIDS	
													Prs	Abd	a	
Azerbaijan	AZE	84	3	0	1	4	64	12	0	0	5	76	1.0	7.4	↑	No
Bangladesh	BGD	146	4	0	6	14	113	9	0	0	20	122	1.0	10.5	↓	No
Barbados	BRB	6	0	0	0	1	5	0	0	0	1	5	**0.1**	3.0	↑	Yes
Belize	BLZ	111	3	0	3	2	98	5	0	0	5	103	1.0	5.2	↑	Yes
Benin	BEN	144	7	0	1	3	124	9	0	0	4	133	1.0	10.3	↑	No
Bhutan	BTN	154	6	1	9	16	108	14	0	0	26	122	-	-		No
Bolivia	BOL	397	31	2	9	10	327	18	0	0	21	345	1.0	56.2	↑	No
Bosnia and Herzegovina	BIH	75	2	0	0	4	62	7	0	0	4	69	1.0	4.2	↑	No
Botswana	BWA	177	2	1	1	4	162	7	0	0	6	169	1.0	8.9	↑	No
Brazil	BRA	625	87	9	29	37	439	24	3	0	75	463	1.0	130.8	↑	No
Brunei Darussalam	BRN	171	17	1	7	25	107	14	0	0	33	121	1.0	11.1	↓	No
Bulgaria	BGR	74	2	0	0	5	60	7	0	0	5	67	1.0	4.3	↓	No
Burkina Faso	BFA	130	6	0	2	4	111	7	0	1	6	118	1.0	8.7	↑	No
Burundi	BDI	202	3	1	2	10	173	13	0	0	13	186	1.0	8.1	↓	No
Cambodia	KHM	158	3	0	14	15	117	9	0	0	29	126	1.0	12.5	↓	No
Cameroon	CMR	318	22	3	16	17	248	12	0	0	36	260	1.0	21.4	↓	No
Canada	CAN	140	0	1	1	1	136	1	0	0	3	137	1.0	3.6	↑	No
Central African Republic	CAF	258	16	1	2	2	226	11	0	0	5	237	-	-		No
Chad	TCD	118	3	2	2	4	101	6	0	1	8	107	-	-		No
Chile	CHL	109	9	3	5	8	76	8	0	0	16	84	1.0	6.0	↓	No
China	CHN	497	43	6	28	32	362	26	0	1	66	388	1.0	118.3	↑	No
Colombia	COL	445	45	5	13	29	338	15	0	0	47	353	1.0	54.5	↑	No
Comoros	COM	6	2	0	1	1	2	0	0	0	2	2	-	-		Yes
Congo, Dem. Rep.	ZAR	446	42	4	9	13	358	20	0	0	26	378	-	-		No
Congo, Rep.	COG	244	20	2	2	6	204	10	0	0	10	214	1.0	14.7	↑	No
Costa Rica	CRI	169	8	0	2	2	146	11	0	0	4	157	1.0	9.5	↑	No
Cote d'Ivoire	CIV	224	17	1	6	12	175	13	0	0	19	188	1.0	15.4	↓	No
Croatia	HRV	79	1	0	0	3	67	8	0	0	3	75	1.0	3.7	↑	No
Cuba	CUB	33	0	3	4	3	20	3	0	0	10	23	-	-		Yes
Cyprus	CYP	21	0	0	0	2	17	2	0	0	2	19	1.0	6.2	↑	No
Czech Republic	CZE	59	0	0	0	1	52	6	0	0	1	58	0.8	3.8	↑	No
Djibouti	DJI	56	2	0	0	3	46	5	0	0	3	51	1.0	2.0	↓	No
Dominica	DMA	11	0	0	0	1	10	0	0	0	1	10	0.9	-		Yes
Dominican Republic	DOM	17	0	0	2	1	13	1	7	0	3	14	0.9	2.5	↓	Yes
Ecuador	ECU	346	37	1	7	30	251	20	3	0	38	271	1.0	26.9	↓	No
Egypt, Arab Rep.	EGY	87	4	0	1	9	70	3	0	1	10	73	1.0	10.5	↑	No

Country	Code	TOT	DD	CR	EN	VU	LC	NT	EX	EW	Thr.	Non-thr	Prediction			SIDS
													Prs	Abd	a	
El Salvador	SLV	107	4	0	2	1	95	5	0	0	3	100	1.0	5.4	↑	No
Equatorial Guinea	GNQ	172	6	3	6	7	143	7	0	0	16	150	-	-		No
Eritrea	ERI	84	2	0	0	2	76	4	0	0	2	80	-	-		No
Ethiopia	ETH	237	16	1	6	11	193	10	0	0	18	203	1.0	21.0	↑	No
Fiji	FJI	6	0	1	2	1	1	1	0	0	4	2	0.6	3.9	↓	Yes
France	FRA	305	16	0	2	14	256	17	1	0	16	273	1.0	30.9	↑	No
Gabon	GAB	183	10	1	1	7	156	8	0	0	9	164	1.0	8.8	↓	No
Gambia, The	GMB	94	3	0	1	1	87	2	0	0	2	89	1.0	3.2	↑	No
Georgia	GEO	84	1	0	2	3	67	11	0	0	5	78	1.0	6.0	↑	No
Ghana	GHA	194	16	0	2	5	161	10	0	0	7	171	1.0	9.5	↑	No
Gibraltar	GIB	35	0	0	0	2	27	6	0	0	2	33	-	-		No
Greece	GRC	86	5	0	0	6	69	6	0	0	6	75	1.0	5.4	↓	No
Greenland	GRL	6	0	0	0	1	5	0	0	0	1	5	-	-		No
Guam	GUM	1	0	0	1	0	0	0	1	0	1	0	-	-		Yes
Guatemala	GTM	166	6	2	4	7	136	11	0	0	13	147	1.0	11.5	↓	No
Guinea	GIN	190	11	1	6	8	152	12	0	0	15	164	-	-		No
Guinea-Bissau	GNB	100	1	0	2	3	90	4	0	0	5	94	1.0	-		Yes
Guyana	GUY	235	18	0	1	6	204	6	0	0	7	210	1.0	12.4	↑	Yes
Haiti	HTI	17	0	0	2	1	13	1	8	0	3	14	**0.3**	3.1	↑	Yes
Honduras	HND	151	5	0	4	1	132	9	1	0	5	141	1.0	8.9	↑	No
Hungary	HUN	66	2	0	0	1	55	8	0	0	1	63	1.0	4.3	↑	No
India	IND	352	16	7	31	44	229	25	0	0	82	254	1.0	53.6	↓	No
Indonesia	IDN	649	118	20	64	93	313	41	1	0	177	354	1.0	373.1	↑	No
Iran, Islamic Rep.	IRN	143	10	0	1	9	110	13	0	0	10	123	-	-		No
Iraq	IRQ	70	2	0	1	6	56	5	1	0	7	61	1.0	-		No
Israel	ISR	81	2	0	0	6	68	5	0	0	6	73	1.0	3.7	↓	No
Italy	ITA	86	2	0	0	5	71	8	1	0	5	79	1.0	5.6	↑	No
Jamaica	JAM	19	0	1	0	2	16	0	1	0	3	16	0.9	-		Yes
Japan	JPN	93	1	3	11	2	70	6	0	0	16	76	1.0	10.4	↓	No
Jordan	JOR	73	2	0	0	6	59	6	0	0	6	65	1.0	2.8	↓	No
Kazakhstan	KAZ	145	6	1	1	5	122	10	0	0	7	132	1.0	11.4	↑	No
Kenya	KEN	354	24	4	7	11	289	19	0	0	22	308	1.0	46.1	↑	No
Korea, Dem. Rep.	PRK	65	3	0	0	4	53	5	0	0	4	58	-	-		No
Korea, Rep.	KOR	48	3	0	0	4	37	4	0	0	4	41	**0.1**	2.9	↓	No
Kuwait	KWT	28	0	0	0	1	24	3	1	0	1	27	0.6	3.3	↑	No
Kyrgyz Republic	KGZ	72	1	0	1	3	63	4	0	0	4	67	1.0	6.5	↑	No
Lao PDR	LAO	214	14	4	16	19	153	8	0	0	39	161	1.0	18.6	↓	No

Country	Code	TOT	DD	CR	EN	VU	LC	NT	EX	EW	Thr.	Non-thr	Prediction			SIDS
													Prs	Abd	a	
Lebanon	LBN	59	1	0	0	3	51	4	0	0	3	55	1.0	1.5	↓	No
Lesotho	LSO	97	0	1	1	2	88	5	0	0	4	93	1.0	2.0	↓	No
Liberia	LBR	174	13	0	5	10	134	12	0	0	15	146	1.0	8.3	↓	No
Libya	LBY	59	4	0	1	4	47	3	0	1	5	50	1.0	7.0	↑	No
Macedonia, FYR	MKD	68	2	0	0	4	58	4	0	0	4	62	0.7	3.5	↓	No
Madagascar	MDG	195	52	6	27	25	75	10	4	0	58	85	1.0	29.9	↓	No
Malawi	MWI	206	10	1	1	3	183	8	0	0	5	191	-	-		No
Malaysia	MYS	303	37	2	20	41	174	29	0	0	63	203	1.0	30.1	↓	No
Mali	MLI	132	6	1	2	5	112	6	0	1	8	118	1.0	7.1	↓	No
Mauritania	MRT	74	3	1	0	2	65	3	0	1	3	68	-	-		No
Mauritius	MUS	4	0	1	1	1	1	0	1	0	3	1	0.8	8.7	↑	Yes
Mexico	MEX	454	11	21	38	22	340	22	5	0	81	362	1.0	65.3	↓	No
Micronesia, Fed. Sts.	FSM	2	0	0	0	2	0	0	0	0	2	0	-	-		Yes
Moldova	MDA	59	1	0	1	1	50	6	0	0	2	56	0.8	3.6	↑	No
Monaco	MCO	43	0	0	0	1	36	6	0	0	1	42	-	-		No
Mongolia	MNG	115	1	1	3	3	101	6	0	0	7	107	1.0	6.7	↓	No
Montenegro	MNE	69	2	0	0	3	59	5	0	0	3	64	-	-		No
Morocco	MAR	79	1	1	3	5	59	10	0	1	9	69	1.0	6.7	↓	No
Mozambique	MOZ	231	9	1	2	5	205	9	0	0	8	214	1.0	10.2	↑	No
Myanmar	MMR	294	21	1	18	27	212	15	0	0	46	227	1.0	-		No
Namibia	NAM	188	1	1	1	5	172	8	0	0	7	180	1.0	15.3	↑	No
Nepal	NPL	176	6	0	10	14	132	14	0	0	24	146	1.0	16.7	↓	No
Netherlands Antilles	ANT	6	0	0	0	1	5	0	1	0	1	5	**0.2**	-		No
New Caledonia	NCL	9	1	1	2	3	2	0	0	0	6	2	0.8	-		No
New Zealand	NZL	3	0	0	0	2	1	0	0	0	2	1	**0.5**	5.5	↑	No
Nicaragua	NIC	148	5	0	2	0	133	8	0	0	2	141	1.0	6.6	↑	No
Niger	NER	110	3	2	1	5	93	6	0	1	8	99	1.0	8.6	↑	No
Nigeria	NGA	245	12	3	4	11	203	12	0	1	18	215	1.0	13.8	↓	No
Northern Mariana Islands	MNP	1	0	0	1	0	0	0	0	0	1	0	-	-		No
Norway	NOR	49	0	0	0	1	46	2	0	0	1	48	0.6	3.8	↑	No
Oman	OMN	43	1	0	1	3	35	3	0	0	4	38	0.9	5.5	↑	No
Pakistan	PAK	161	4	0	5	7	134	11	0	0	12	145	1.0	15.2	↑	No
Panama	PAN	188	15	1	2	2	157	11	0	0	5	168	1.0	11.0	↑	No
Papua New Guinea	PNG	249	35	11	18	10	165	10	0	0	39	175	1.0	33.2	↓	Yes
Paraguay	PRY	179	14	0	3	5	140	17	0	0	8	157	1.0	9.2	↑	No
Peru	PER	455	42	2	12	36	342	21	2	0	50	363	1.0	70.3	↑	No

Country	Code	TOT	DD	CR	EN	VU	LC	NT	EX	EW	Thr.	Non-thr	Prediction			SIDS
													Prs	Abd	a	
Philippines	PHL	157	24	4	9	17	88	15	0	0	30	103	1.0	18.5	↓	No
Portugal	PRT	53	0	0	2	3	40	8	0	0	5	48	1.0	4.3	↓	No
Puerto Rico	PRI	11	0	0	0	2	9	0	2	0	2	9	-	-		No
Qatar	QAT	18	0	0	0	1	16	1	0	0	1	17	-	-		No
Romania	ROM	77	2	0	1	4	60	10	0	0	5	70	0.9	5.3	↑	No
Russian Federation	RUS	227	10	1	6	9	181	20	0	0	16	201	1.0	11.7	↓	No
Rwanda	RWA	236	4	2	4	12	200	14	0	0	18	214	1.0	14.3	↓	No
Sao Tome and Principe	STP	7	1	0	3	0	3	0	0	0	3	3	1.0	-		No
Saudi Arabia	SAU	58	1	0	0	3	50	4	1	0	3	54	1.0	6.7	↑	No
Senegal	SEN	129	4	0	3	3	114	5	0	1	6	119	1.0	8.1	↑	No
Serbia	SRB	79	3	0	0	4	64	8	0	0	4	72	-	-		No
Seychelles	SYC	5	0	1	0	1	3	0	0	0	2	3	0.9	5.0	↑	Yes
Sierra Leone	SLE	141	6	0	3	3	118	11	0	0	6	129	1.0	5.1	↓	No
Singapore	SGP	53	1	0	3	4	39	6	0	0	7	45	1.0	5.9	↓	Yes
Slovak Republic	SVK	70	2	0	0	1	59	8	0	0	1	67	0.7	4.7	↑	No
Slovenia	SVN	68	2	0	0	1	58	7	0	0	1	65	1.0	5.7	↑	No
Solomon Islands	SLB	45	6	2	8	4	24	1	0	0	14	25	0.9	13.8	↓	Yes
Somalia	SOM	147	10	1	2	5	121	8	0	0	8	129	-	-		No
South Africa	ZAF	260	8	3	6	11	222	10	1	0	20	232	1.0	15.7	↓	No
Spain	ESP	89	1	1	3	6	68	10	0	0	10	78	1.0	5.9	↓	No
Sri Lanka	LKA	82	0	0	11	10	55	6	0	0	21	61	1.0	23.1	↑	No
Sudan	SDN	289	18	1	4	6	248	12	0	1	11	260	1.0	23.4	↑	No
Suriname	SUR	208	14	0	1	4	183	6	0	0	5	189	1.0	7.7	↑	Yes
Swaziland	SWZ	148	1	1	2	1	137	6	0	0	4	143	1.0	5.3	↑	No
Switzerland	CHE	71	2	0	0	1	61	7	0	0	1	68	1.0	4.2	↑	No
Syrian Arab Republic	SYR	79	2	0	0	6	65	6	0	0	6	71	1.0	7.9	↑	No
Tajikistan	TJK	75	2	0	1	3	63	6	0	0	4	69	0.8	5.7	↑	No
Tanzania	TZA	357	14	5	14	12	292	20	0	0	31	312	1.0	40.7	↑	No
Thailand	THA	265	20	0	17	27	176	25	1	0	44	201	1.0	31.3	↓	No
Timor-Leste	TMP	42	10	0	0	2	29	1	0	0	2	30	-	-		Yes
Togo	TGO	152	8	0	0	3	133	8	0	0	3	141	1.0	8.2	↑	No
Tunisia	TUN	57	2	0	2	3	45	5	0	1	5	50	1.0	5.3	↑	No
Turkey	TUR	128	8	0	1	9	98	12	0	0	10	110	1.0	9.9	↓	No
Turkmenistan	TKM	76	2	0	0	3	65	6	0	0	3	71	-	-		No
Uganda	UGA	349	18	1	8	14	288	20	0	0	23	308	1.0	38.0	↑	No
Ukraine	UKR	91	1	0	2	3	76	9	0	0	5	85	1.0	6.5	↑	No
United Arab Emirates	ARE	31	1	0	1	2	25	2	0	0	3	27	-	-		No

Country	Code	TOT	DD	CR	EN	VU	LC	NT	EX	EW	Thr.	Non-thr	Prediction			SIDS
													Prs	Abd	a	
United Kingdom	GBR	59	0	0	0	2	54	3	0	0	2	57	0.6	4.8	↑	No
United States	USA	371	4	2	10	9	332	14	1	0	21	346	1.0	28.7	↑	No
Uruguay	URY	84	4	0	3	1	66	10	0	0	4	76	1.0	4.0	↑	No
Uzbekistan	UZB	82	2	1	1	4	67	7	0	0	6	74	-	-		No
Vanuatu	VUT	11	1	0	2	2	6	0	0	0	4	6	0.9	3.0	↓	Yes
Venezuela, RB	VEN	341	30	3	7	22	270	9	1	0	32	279	1.0	21.9	↓	No
Vietnam	VNM	252	16	9	18	21	177	11	0	0	48	188	1.0	26.9	↓	No
Virgin Islands (U.S.)	VIR	4	0	0	0	1	3	0	1	0	1	3	-	-		No
West Bank and Gaza	WBG	92	2	0	0	7	78	5	0	0	7	83	1.0	3.7	↓	No
Yemen, Rep.	YEM	52	1	0	0	2	45	4	2	0	2	49	1.0	-		No
Zambia	ZMB	255	16	1	2	4	222	10	0	0	7	232	1.0	9.9	↑	No
Zimbabwe	ZWE	216	6	1	1	6	195	7	0	0	8	202	-	-		No

Appendix 2.S4. Results of model predicting presence and abundance of threatened species by country considering data deficient species (DD) as threatened.

Presence of threatened species

The variable selection procedure did not allow obtaining a global minimum adequate model (MAM), since the number of selected variables from categorical models (7 linear; 5 quadratic) was too high for the reduced sample size of countries with none threatened mammals (considering DD species as non-threatened 27 countries had zero threatened species; with DD as threatened that number is reduced to 24). Therefore, we used the selected variables for the model including DD species as non-threatened (Table 2.1 of the main text) and fitted it for the new set of data to check for coincident results.

This model (Table 2.S9) explains 61.3% of the deviance: 34.2% by control variables and 27.1% by the socioeconomic indicators. Performance measures were satisfactory, but lower than in the conservative model (DD as non-threatened) (sensitivity=0.950; specificity=0.759; AUC=0.967).

Table 2.S9. Results of the final model exploring the effect of socioeconomic indicators on the probability of presence of threatened mammals by country (N=162). We report the best coefficient estimate and its standard error [β (SE)] and the mean odds ratio (OR) with the 95 % confidence interval (CI) for all variables in the final model.

Variables	β (SE)	OR (95 %CI)
Socioeconomic		
Urban population^2	-0.00 (0.001)	1.00 (0.998;1.001)
Urban population	0.06 (0.118)	1.06 (0.832;1.332)
Population growth	1.22 (0.570)*	3.40 (1.196;11.597)
Arable land^2	0.00 (0.002)*	1.00 (1.001;1.008)
Arable land	-0.24 (0.095)*	0.78 (0.633;0.929)
Tourism receipts^2	-0.01 (0.002)**	0.99 (0.990;0.998)
Tourism receipts	0.42 (0148)**	1.53 (1.198;2.160)
Control		
Total mammals	0.13 (0.037)***	1.14 (1.074;1.244)

Land area	0.00 (0.000)	1.00 (1.000;1.000)
Shared mammals	-0.81 (1.638)	0.44 (0.017;11.033)

[2] squared-root transformation; ***P<0.001, **P<0.01, *P<0.05, · P< 0.1

Abundance of threatened species

The final MAM (Table 2.S10) includes the same variables as the MAM considering DD species as non-threatened (Table 2.2 of the main text) and adds three more: population growth (% annual), CO_2 emissions and international expenditures on tourism (% imports). A rapidly growing country, with relatively low CO_2 emissions and extreme (either very low or very high) levels of international tourism expenditures appears also more susceptible to harbor higher numbers of threatened mammals (Fig. 2.S9), which generally agrees with the profile of countries described in the main text. This model (Table 2.S10) explains 85.3% of the deviance: 77.3% by control variables and 8.0% by socioeconomic indicators. Predictions errors are within a ±0.33% of total mammal richness per country, with four countries being estimated over this value: Indonesia, Seychelles, New Zealand and Mauritius.

Table 2.S10. Results of the final model exploring the effect of socioeconomic indicators on the abundance of threatened mammals by country (N=127). We report the best coefficient estimate and its standard error [β (SE)] for all variables in the final model.

Variables	β (SE)
Socioeconomic	
Urban population	-0.01 (0.003)·
Imports GS	-0.01 (0.004)**
Exports GS	0.01 (0.004)**
Life expectancy[2]	-0.00 (0.000)*
Life expectancy	0.16 (0.062)**
Tourism receipts[2]	-0.00 (0.000)***
Tourism receipts	0.03 (0.013)*
Tourism expenditures2	0.00 (0.002)*
Tourism expenditures	-0.08 (0.041)·
Population growth	0.15 (0.054)**
CO_2 emissions	-0.04 (0.014)**
Control	

Total mammals	0.01 (0.000)***
Land area	0.00 (0.000)
Shared mammals	-0.74 (0177)***

[2] squared-root transformation; ***P<0.001, **P<0.01, *P<0.05, · P< 0.1

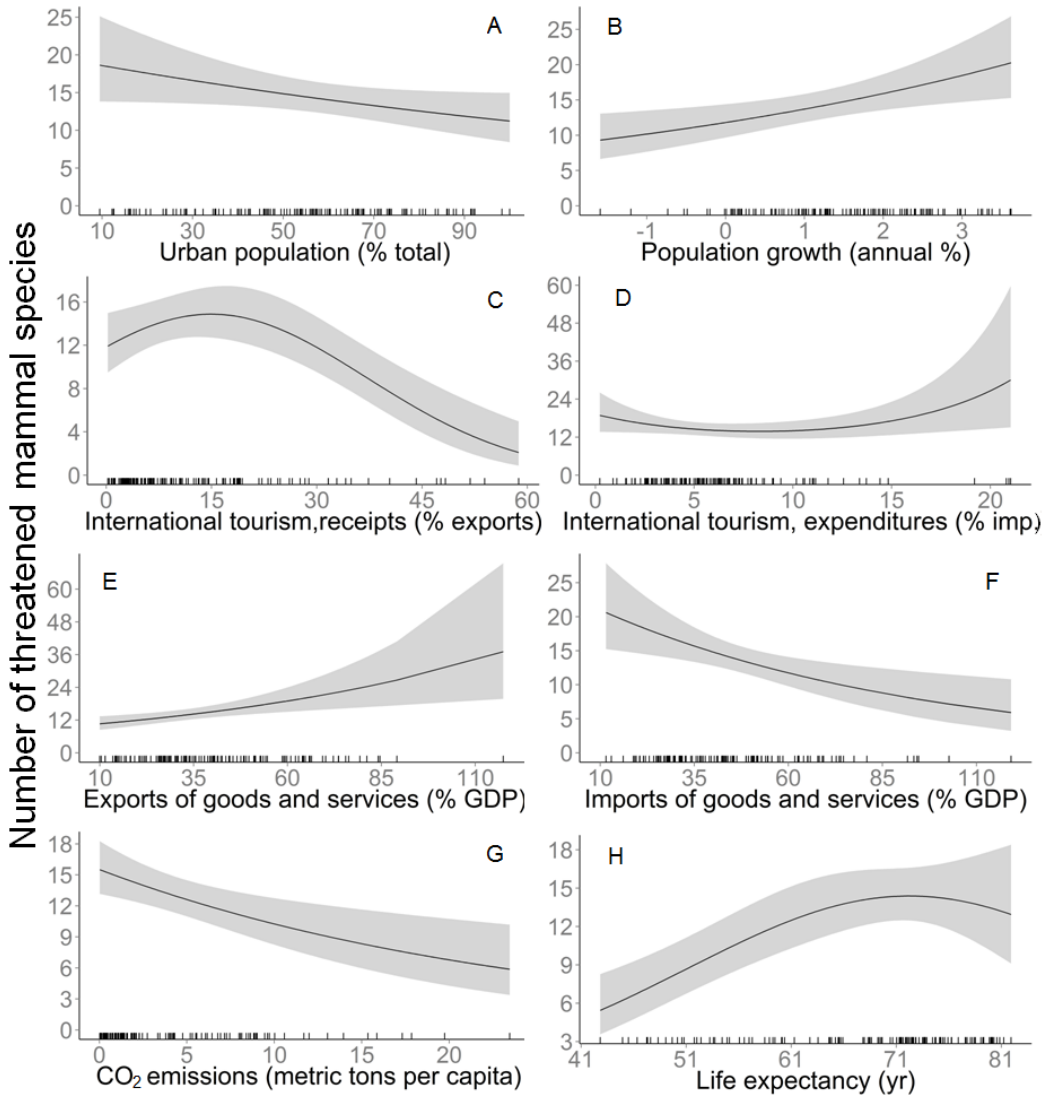


Figure 2.S1. Predicted relationships between key socioeconomic variables and the abundance of threatened mammals by country (DD species classified as threatened). Model predictions were based on the final model (Table 2.S10) and estimated by exploring the range of observed values for each indicator while using the median observed value for other variables in the model (Median values: total mammal richness = 129; land area = 192,530 sq·km; percentage of shared species = 0.759; urban population = 55.90%; population growth = 1.32%; international tourism, receipts = 9.18% exports; international tourism, expenditures = 5.43% imports; exports of goods and services =36.45% GDP; imports of goods and services = 42.64% GDP; CO2 emissions = 1.872

metric tons per capita; life expectancy = 71.38). Shadowed area represents the confidence intervals (95%). Singapur was removed from graphs E and F to facilitate visualization, given the extremely high values it presents for these two indicators (imports of goods and services (% GDP)= 200.452; exports of goods and services (% GDP)= 228.007). Kuwait was removed from graph G (CO_2 emissions = 35.42 metric t per capita).

Appendix 2.S5. Geographic representation of the estimated values for all variables included in any final model. We show values for all countries with data available on the World Bank database even those not included in the final models (due to missing data on some of the selected variables).

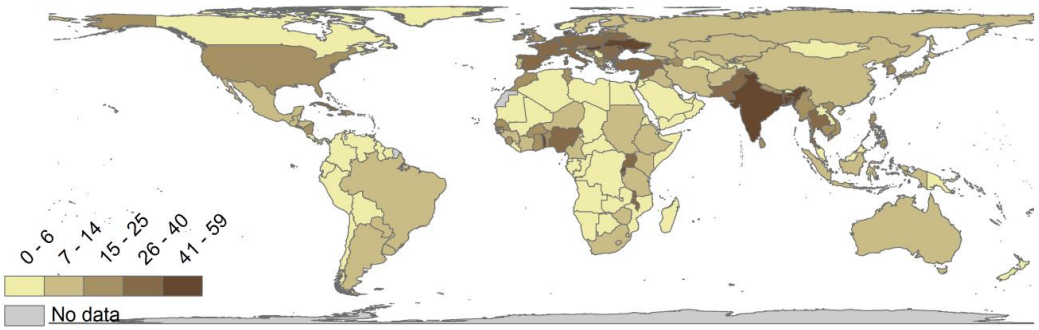


Figure 2.S2. Arable land (% total land)

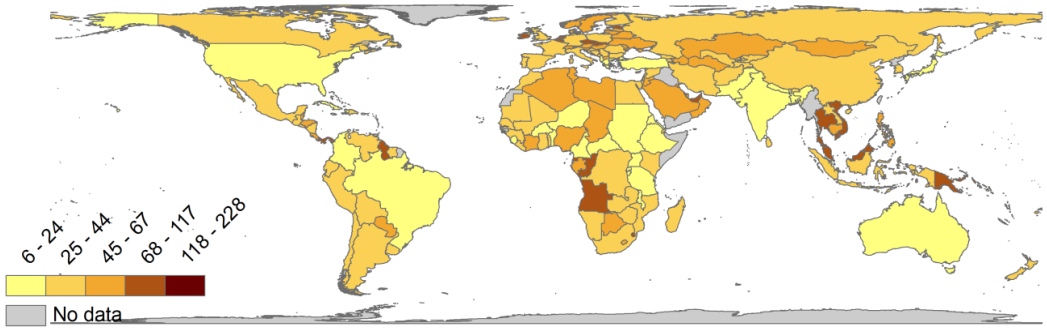


Figure 2.S3. Exports of goods and services (% GDP)

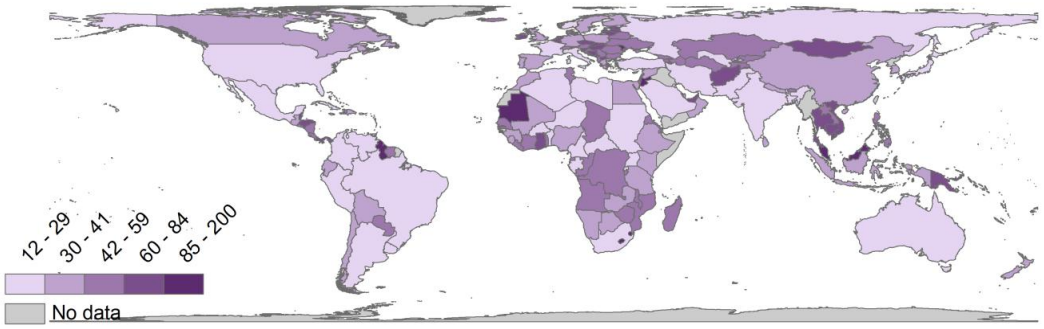


Figure 2.S4. Imports of goods and services (% GDP)

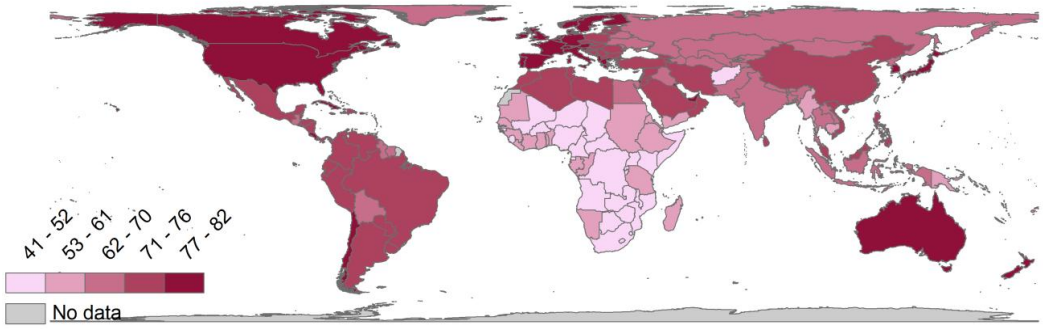


Figure 2.S5. Life expectancy (years)

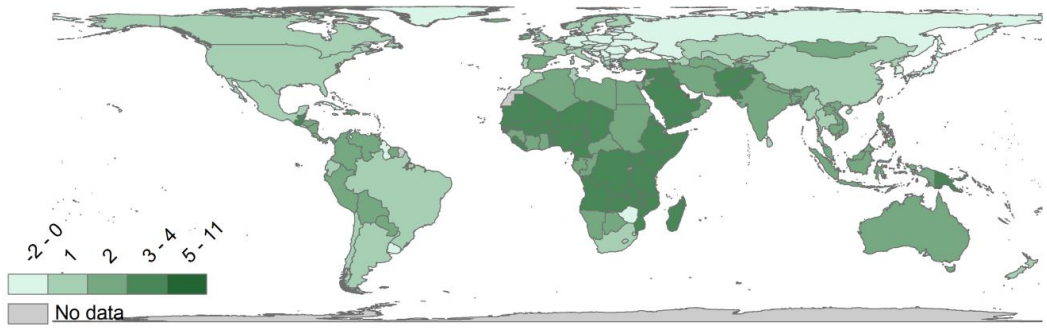


Figure 2.S6. Population growth (annual %)

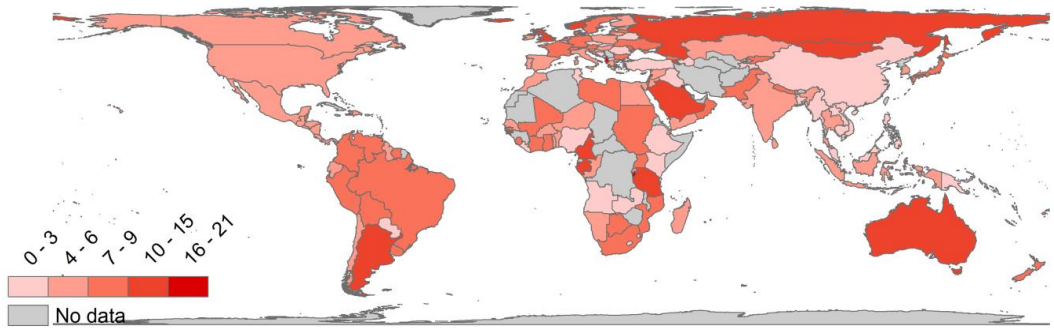


Figure 2.S7. International tourism, expenditures (% imports)

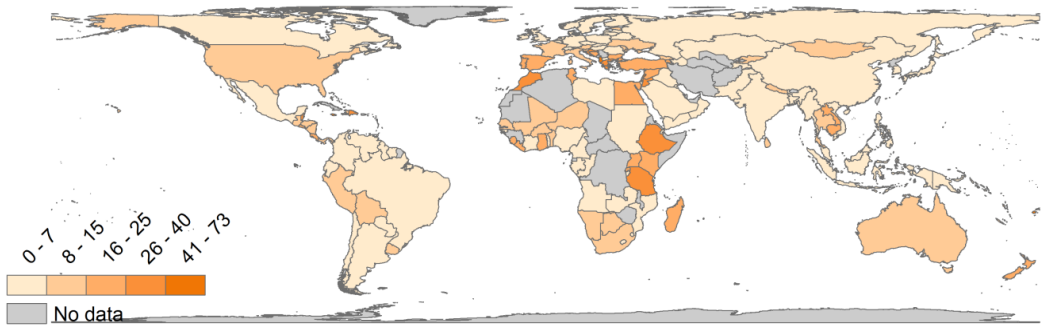


Figure 2.S8. International tourism, receipts (% exports)

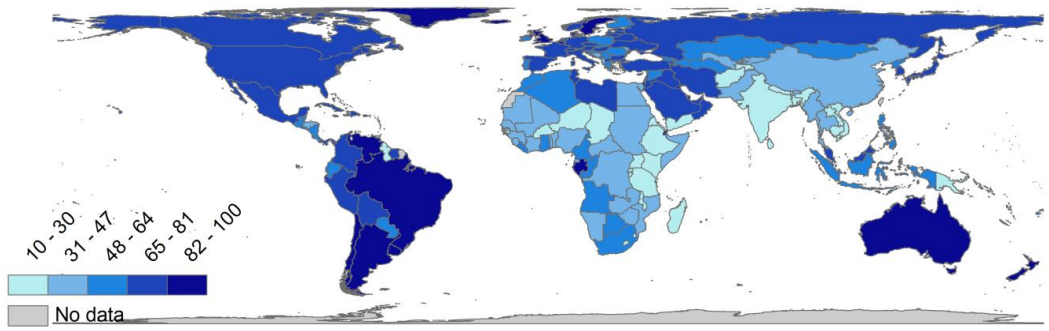


Figure 2.S9. Urban population (% total)

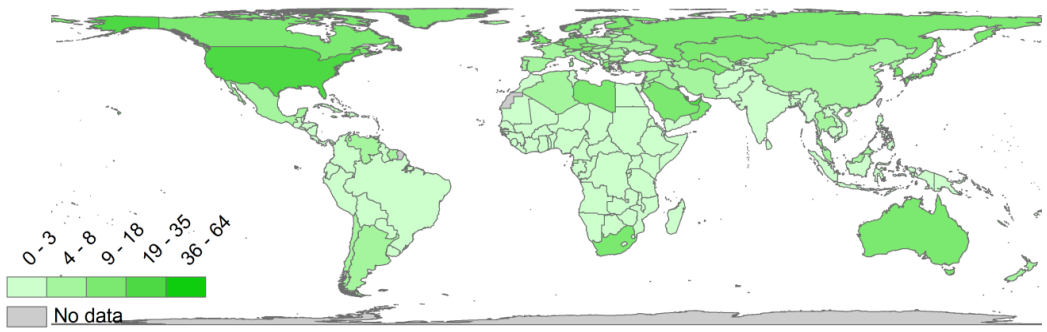
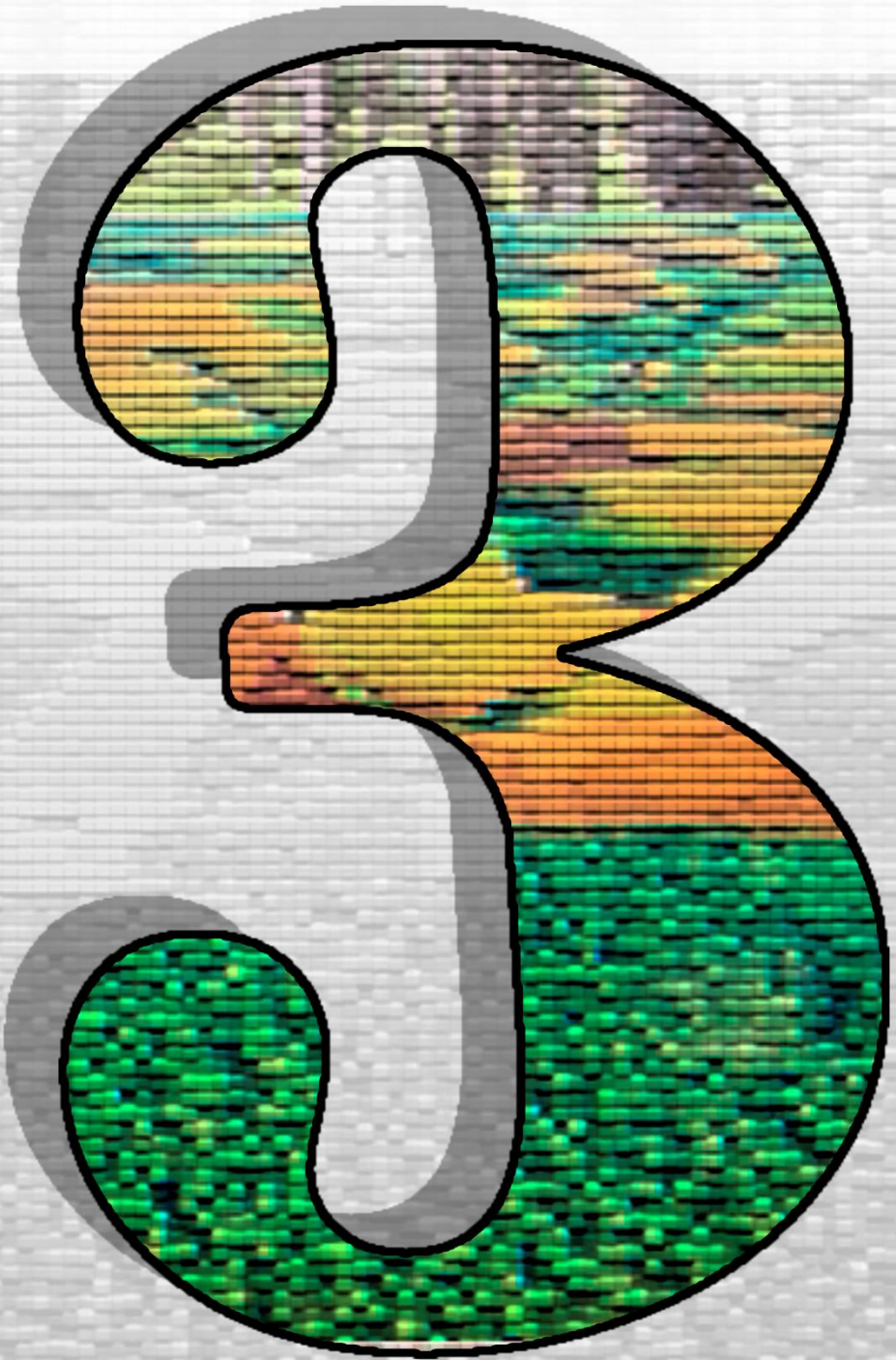


Figure 2.S10. CO_2 emissions per capita (metric tons per capita)

The implications of land-use extent and intensity for global mammalian conservation



Polaina, E., González-Suárez, M., Kuemmerle, T., Kehoe, L. and Revilla, E. The implications of land-use extent and intensity for global mammalian conservation (*In prep*).

Abstract

Event today, the way agricultural land use affects biodiversity on a global scale is not fully understood. This is worrisome given that agriculture is the main threat for terrestrial vertebrates. In the present work, we test which metrics of land use, specifically its extent, intensity or history, are better able to explain currently threatened mammals' distribution. Additionally, we untangle the relationships between these land-use indicators and the proportion of threatened mammals using boosted regression trees (BRT). We test two broad alternative hypotheses, first globally and then by biogeographic realm: one assuming that threatened species should concentrate in relatively low-intensity areas (*refuge* hypothesis), and the other postulating that threatened species should concentrate in areas of high human pressure (*threat* hypothesis). Our results show that there is no predominant metric of land use that best explains the distribution of threatened species, although forest cover (land-use extent) plays an important role. The two anticipated hypotheses are alternatively (and simultaneously) confirmed in different regions, which may be related to different agricultural stages of development. Thus, we propose both hypotheses could be integrated into a single continuous hypothesis including a new type of areas, *'new' threat* areas, which have already undergone a long trajectory of human impact, and where threatening activities and threatened mammals spatially coincide. We conclude that multiple land-use metrics are needed to understand relationships between agriculture and biodiversity at the global scale, and that separating regions according to their human and biogeographic characteristics is beneficial to disentangle these patterns. Using this comprehensive approach will facilitate the identification of global threats and the definition of effective conservation measures.

Resumen

Cómo el uso agrícola del suelo afecta a la biodiversidad a escala global sigue sin ser completamente entendido a día de hoy. Esto es preocupante, dado que la agricultura es la principal amenaza para los vertebrados terrestres. En el presente trabajo, probamos qué métricos de uso del suelo, concretamente en relación a su extensión, intensidad e historia, son capaces de explicar mejor la actual distribución de los mamíferos terrestres; además, desentrañamos las relaciones entre estos indicadores de uso del suelo y la proporción de mamíferos amenazados, utilizando árboles de regresión impulsados (*boosted regression trees,* BRT). Considerando dos escalas, global y de reino biogeográfico, examinamos dos hipótesis generales y alternativas: una asume que más especies amenazadas deberían concentrarse en áreas relativamente poco usadas (hipótesis *refugio*), y la otra postula que más especies amenazadas se concentran en áreas de alta presión humana (hipótesis *amenaza*). Nuestros resultados muestran que no hay un único tipo de métrico que predomine sobre el resto, aunque la cobertura de bosque juega un papel importante (extensión del uso). Las dos hipótesis propuestas se confirman de manera alternativa en distintas regiones (y también simultáneamente), lo cual podría estar relacionado con distintos estadios de desarrollo agrícola. Así, proponemos que ambas hipótesis podrían ser integradas en una sola hipótesis continua que, además, incluye un nuevo tipo de áreas: áreas de *'nueva' amenaza*, las cuales se han visto sometidas a una larga trayectoria de impacto humano, y donde actividades amenazantes y mamíferos amenazados coinciden espacialmente. Se concluye que es necesario incluir distintos indicadores de uso del suelo para entender las relaciones entre agricultura y conservación de la biodiversidad a escala global, y que separar regiones de acuerdo a sus características humanas y biogeográficas supone una ventaja para realmente comprender estos patrones. De esta manera, la identificación de amenazas globales y medidas de conservación efectivas se verá favorecida.

Introduction

Agriculture is the most common threat for terrestrial vertebrates (Salafsky et al. 2008; González-Suárez et al. 2013; IUCN 2014; Böhm et al. 2016), now occupying more than 38% of all ice-free land across the world (FAOSTAT 2011). Agriculture affects biodiversity in various, typically detrimental ways, for example via habitat loss, deterioration or fragmentation (Millenium Ecosystem Assessment 2005; Gasparri & Grau 2009; González-Suárez & Revilla 2014), but also with less evident effects such as the destabilization of ecological interactions (Fontúrbel et al. 2015) or facilitating the introduction of non-native species (Vilà et al. 2011). During the 20th century and the early 2000's most of the growth in agricultural production was a consequence of global intensification. However, agricultural expansion still occurred, primarily in South Asia, Central and South America and Africa (Ramankutty et al. 2002; Evenson & Gollin 2003; Grassini et al. 2013), often at the expense of key natural areas (Gibbs et al. 2010). During this period there were also localized reductions in agricultural extension due to land abandonment in some areas of Europe and North America. Agriculture is essential to humanity, and the demand for food, fiber and biofuels will further increase due to the rapidly growing human population, increasing per-capita consumption, and modification of human diet that is ongoing since the mid-20th century (Bloom 2011; UN 2014; Kastner et al. 2012; Machovina & Feeley 2014). Global projections suggest noticeable agricultural expansion with a 10–25% increase in cropland extension by 2050 (respect to 2005; Schmitz et al. 2014). Given its current importance and likely future expansion, understanding how agriculture threatens biodiversity and which aspects of agriculture are contributing most to these threats is crucial to achieve the preservation of part of the remaining biodiversity.

The effects of agricultural expansion and intensification on biodiversity are varied, and can be difficult to differentiate because expansion and intensification often occur simultaneously. Many studies have empirically demonstrated that biodiversity decreases as agriculture expands into natural areas (Kerr & Deguise 2004; Koh & Wilcove 2008). It is also clear that increased intensification negatively affects species by reducing their areas of occupancy, disrupting community composition, and

decreasing functional diversity (Donald et al. 2001; Flynn et al. 2009; Kleijn et al. 2009; Newbold et al. 2015). However, most studies have focused on local or regional scales, single indicators or have not simultaneously assessed the effects of extent and intensity of agriculture. Therefore, we lack a global perspective of how different agricultural land uses and intensification patterns, including different intensity metrics, relate to biodiversity loss and endangerment (Kehoe et al. 2015).

In addition, a more comprehensive perspective would also need to consider historical factors. Current biodiversity patterns have likely been altered by past land uses (Dupouey et al. 2002; Ellis et al. 2010) which may have directly resulted in extinctions and declines (Balmford 1996), and indirectly modified biotic and abiotic conditions with long-lasting, and possibly lagged, effects on ecosystems (Foster et al. 2003; Dullinger et al. 2013). Areas with a history of profound land use might have already lost their most sensitive species and/or present sub-optimal habitat conditions. However, few studies have considered how the past history of land use influences current biodiversity. All in all, we need a better understanding of how different indicators of land use including current land-use extent, intensity, and history associate with current biodiversity patterns.

There is not a universal metric of conservation status of biodiversity, due to the difficulty of capturing the complexity of environmental and human processes that have triggered current patterns (Ceballos & Brown 1995; Lamoreux et al. 2006). However, when exploring human threats, it seems reasonable to use a metric that incorporates knowledge on how well or poorly preserved species are, like the number (or percentage) of threatened species. This indicator has been used in conservation planning for priority area selection (Bonn et al. 2002; Grenyer et al. 2006) indirectly assuming that areas where threatened species remain include the environmental conditions that allow for their persistence, thus are relatively unused. More intensely (or longer) used areas would have already lost most sensitive species, thus fewer threatened species would be found (Fig. 3.1 II; Sandom et al. 2014; Polaina et al. 2015). The relationship between land-use extent, intensity or time of use and number of threatened species is therefore expected to be negative, and we will refer to this as the *refuge* hypothesis. On the other hand, some authors (e.g. Lenzen et al. 2009) have

postulated a positive relationship in which the greater number of threatened species and the most threatening activities coincide (*threat* hypothesis; Fig. 3.1 I). These authors postulate that areas with limited human use are relatively well preserved and thus, harbor fewer threatened species, while in extensively/intensely used areas vulnerable species become threatened.

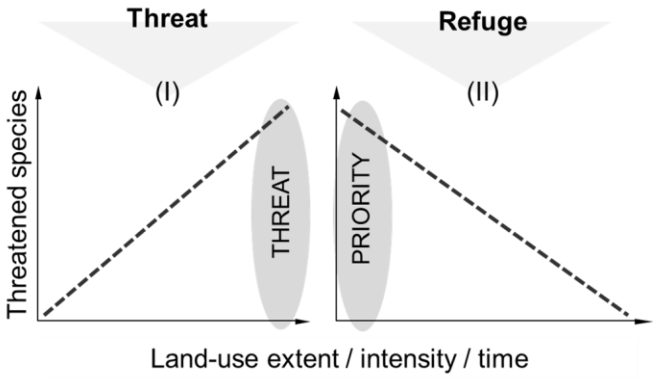


Figure 3.1. Conceptual summary of the two main hypotheses proposed: *threat* (I) and *refuge* (II).

This study aims to provide a better understanding of how different indicators of land use are associated with current mammalian biodiversity patterns, defined as the proportion of threatened terrestrial mammals in different regions of the world. We focus on terrestrial mammals because their conservation status is generally well defined by the IUCN Red List (IUCN 2014) and because most species in this group are affected by agricultural land transformation (González-Suárez & Revilla 2014). Our first objective is to evaluate which of the three types of land-use indicators, extent, intensity or history, better explains threatened mammals' current distributions at both the global and biogeographic-realms scale. Our second objective is to test the support for each hypothesis describing the relationship between land-use indicators and the proportion of threatened species: *threat* or *refuge*.

Methods

Data sources

Terrestrial mammal species' distributions were obtained from the International Union for Conservation of Nature (IUCN 2014), selecting only native, extant and probably extant areas. These data include 18% of mammals classified as threatened (vulnerable, endangered or critically endangered), 69% as not-threatened (least concern or near threatened), and 13% as data deficient. Distribution data were intersected with a grid, and species were considered as present in a particular grid cell when any overlap existed. The grid was defined using a Berhmann cylindrical, equal-area projection, where each grid cell corresponds to approximately 110 x 110 km (= 12,100 km², ~1x1º near the equator). We only selected cells that contain cropland as defined by Erb et al.'s (2007) classification (see more details below), and at least 10,000 km² of emerged land area (avoiding edge grid cells, which would add unequal sample sizes in the analyses).

To describe land use, we considered three groups of variables: land-use extent, land-use intensity and land-use history (Tables 3.1 and 3.S1). The global land use classification of Erb et al. (2007) was employed to define different percentages of land use within each grid cell including five categories: cropland, forest, grazing land, urban and infrastructure, and areas without defined land use (remaining surface not classified under any of the other categories). We chose this classification because all categories sum up to 100% of the grid surface, it is coherent with national census data and most of the intensity metrics we used are based on these cropland data.

We selected indicators of land-use intensity based on the conceptual framework of Erb et al. (2013), including measures of inputs (irrigated area and fertilizer added) and outputs (yields of maize, wheat and rice, as well as harvested area of soy and oil palm; Tables 3.1 and 3.S1). Input metrics reflect direct potential impacts to nutrient and water cycles and are often employed when assessing biodiversity responses (McLaughlin & Mineau 1995; García de Jalón et al. 2013). Outputs are actual measures of productivity, thus deemed to better represent intensity of use (Turner & Doolittle 1978). We selected yields of maize, wheat and rice because these are the dominant global cereal production crops (Hafner 2003). Representing each crop separately is important to capture regional differences in productivity among areas where one crop may be largely absent but others are dominant (Table 3.1). Finally, soy and palm oil crops are increasingly relevant in the tropics, where plantations are

expanding at the expense of primary forests (Hecht 2005; Gutiérrez-Vélez et al. 2011) and where mammalian biodiversity is higher (Ceballos & Ehrlich 2006). We used available data on harvested area of soybeans and palm oil rather than yields (Monfreda et al. 2008) because they were more consistent among alternative data sources (Fitzherbert et al. 2008; GAEZ 2010; Ray et al. 2013).

Land-use history was evaluated by including the categorical variable of time since first significant land use (hereafter TFU) following the KK10 model (Kaplan et al. 2011), defined as the time at which more than 20% of a grid-cell is classified as used by humans (Ellis et al. 2013). The KK10 model includes estimations of area converted for any type of human use (e.g. settlements, grazing lands, etc.) based on population densities and per capita use of land, although it does not explicitly incorporate intensity metrics. This data source is considered more realistic than others regarding historical land-use patterns (Ellis et al. 2013; Boivin et al. 2016).

The original resolution of the different datasets varies (Table 3.S1), thus we recalculated mean values per 110 x 110 km grid cell using the Zonal Statistics tool within the Spatial analyst extension in ArcGIS 10.3 (ESRI 2011).

Statistical analyses

The analyzed grid surface was divided into biogeographic realms (based on a modified classification of Olson et al. 2001) including: Afrotropics (1463 grid cells), Australasia (300 grid cells), Indomalay (518 grid cells), Nearctic (994 grid cells) and Neotropics (1463 grid cells). The Palearctic realm was geographically subdivided into Asia (2078 grid cells) and Europe (including Morocco and northern Algeria; 926 grid cells) to reflect their marked differences in terms of human history. All grid cells that were not completely included in any of the mentioned realms were assigned to the Ecotone category and included in the global model, but not considered separately (N=210; grey areas in Fig. 3.2). Madagascar was excluded from the Afrotropics' analysis (but not from the global) given its biogeographic particularities as an island. The defined biogeographic units broadly group areas with similar natural and human history. This enhances our ability to detect patterns without confounding different processes (e.g.

the minimum cover of urban areas in Europe could be the maximum in areas of Australasia).

We performed one global and seven realm-specific models. Realm was included as a categorical variable in the global model to account for the expected differences among realms and, at the same time, to avoid pseudoreplication within grid cells of the same realm. We used the proportion of cover of the different land-use categories, land-use intensity metrics, and TFU by grid cell as predictor variables, and the percentage of threatened mammals (of the total richness) as the response (Tables 3.1 and 3.S1). An "island" dummy explanatory variable was included to account for those grid cells included within an island territory (≥10,000 km², because smaller ones were excluded from the analyses) that may present island-specific vulnerability attributes. Australasia is entirely formed by islands, thus the dummy variable was not included. The response variable was $\log_{10}$ arc-sine transformed to achieve normality (Sokal & Rohlf 1995).

Data were analyzed using a boosted regression tree (BRT) method implemented in the *dismo* package (Hijmans et al. 2013) in R (R Core Team 2014). The function 'gbm.step' calculates the optimal number of boosting trees using 10-fold cross validation. We used a Gaussian error structure, a bagging fraction of 0.5, and a tree complexity of 10. Learning rate was 0.050 for the global model and 0.001 for the biome-specific ones. These parameters were fixed according to the guidelines in Elith et al. (2008) to achieve a minimum of 1000 trees. We considered a particular predictor as relevant when its relative importance was greater than expected due to chance (total importance of 100% divided by the number of variables included in each model; e.g. Müller et al. 2013).

In ecology, unexplained deviance related to space (often considered as spatial autocorrelation) is normally a consequence of environmental factors (Legendre et al. 2002) or ecological constrains, such as the dispersal abilities of species (Wintle & Bardos 2006). To account for spatial autocorrelation in our analyses all models included a residuals-based autocovariate (RAC) that specified the relationship between the value of the residuals at each location and those at neighboring locations (the 8 immediate grid cells surrounding each cell as neighbors, approximately within a

165 km distance in our case). Deriving the autocovariate from the residuals allows for the inclusion of only the remaining unexplained deviance of the explanatory variables, thus the actual influence of the predictors is better captured (Crase et al. 2012). The explanatory power of all models was calculated as the percentage of deviance explained where the null deviance is the initial value before any split is made (Ferrier & Watson 1997).

Results

We completed the analyses on 7,962 grid cells representing around 61% of the global terrestrial surface excluding Antarctica. A total of 4780 terrestrial mammals overlapped the selected study area. Regarding land-use extent variables, our grid cells included varying proportions of croplands, ranging from <0.01% to 57% (5 and 95% quantiles, respectively), with the Indomalay realm having the highest mean value (40%), and the Neotropics the lowest (7.8%, Table 3.1). Within the study surface (world land containing some cropland and excluding continental edges), other land-use extent components presented varying proportions: built-up areas represented the lowest extensions (global average, 1.2%), and grazing lands the greatest (global average, 40.5%). Globally, croplands tended to co-occur with built-up areas (Spearman's ρ=0.67; Table 3.S2) and were moderately complementary to non-used portions (ρ=-0.34; Table 3.S2), although these configurations varied among realms (Tables 3.S3-3.S9). Land-use intensity metrics also presented quite heterogeneous values among realms, with oil palm and soy presenting very low overall harvested areas (Table 3.1). Land-use history, represented by TFU, offered a general idea of the age of human settlements in each of the biogeographic realms, Indomalay being on average the oldest and Australasia the youngest. Mammalian richness showed the expected latitudinal gradient, with relatively high values in the tropics (Afrotropics, Indomalay and Neotropics), and low in temperate regions (Asia, Europe and the Nearctic) and Australasia. Threatened mammalian richness (number of threatened species) was also unevenly distributed across realms but did not show such a clear gradient. The Indomalay and the Neotropics presented high absolute and relative

values, whereas the Afrotropics harbor relatively low values and the Nearctic has the lowest (Table 3.1).

Table 3.1. Global and realm-specific summary of variables of land use extent, intensity and history, and mammalian diversity. All LU original datasets correspond to around year 2000 and have a spatial resolution of 5 min, excepting fertilizer dataset, which have a 10 km resolution (further details in Table 3.S1). All values represent the mean value within each grid cell of ~110x110 km. TFU was converted to continuous for this purpose.

Variables	Mean values per grid cell							
	Global	Afro.	Asia	Austr.	Europe	Indo.	Nearctic	Neotrop.
Land-use extent (portion of grid cell)								
Built-up[1]	0.012	0.005	0.008	0.004	0.032	0.018	0.025	0.003
Cropland[1]	0.141	0.095	0.088	0.126	0.255	0.400	0.178	0.078
Forest[1]	0.319	0.300	0.254	0.239	0.319	0.326	0.325	0.447
Grazing land[1]	0.405	0.558	0.432	0.460	0.304	0.245	0.328	0.375
No used[1]	0.123	0.042	0.218	0.171	0.091	0.011	0.145	0.096
Land-use intensity								
Inputs								
Fertilizer[2] (kg/ha)	6.167	0.552	6.351	2.452	10.915	18.622	8.767	1.927
Irrigated area[3] (portion of grid cell)	2.470	0.312	2.628	0.496	2.810	12.516	2.326	0.624
Outputs								
Maize[4] (tons/ha)	1.703	0.820	1.226	1.568	2.445	1.831	3.419	1.663
Rice[4] (tons/ha)	1.103	1.002	1.129	0.801	0.678	2.712	0.130	1.411
Wheat[4] (tons/ha)	1.052	0.965	0.884	0.514	1.732	1.045	1.709	0.521
Oil palm[4] (portion of grid cell)	0.001	0.002	-	<0.001	-	0.005	-	<0.001
Soy[4] (portion of grid cell)	0.007	0.000	0.003	0.000	0.001	0.011	0.024	0.014
Land-use history								
TFU[5] (years)	626	1185	329	1374	120	-315[6]	1127	651
Mammalian diversity								
Total richness	78.1	106.4	45.5	42.5	49.0	95.0	58.3	130.8
Threatened spp	4.1	4.4	2.4	1.5	1.5	14.3	0.4	6.8
(%)	5%	4%	5%	3%	3%	15%	1%	5%

[1]Erb et al. (2007); [2]Potter et al. (2010); [3]Siebert et al. (2005); [4]Monfreda et al. (2008); [5]Time of first significant use, Ellis et al. (2013); categories: BC6000, BC3000, BC1000, AD0, AD 1000, AD 1500, AD1750, AD1900, AD1950, AD2000, No used. [6]B.C.315

Model performance was overall relatively high, with 82.5% deviance explained by the global BRT, and values ranging from 43.4% (Australasia) to 82.4% (Asia) for the realm-specific BRTs (Table 3.2). The inclusion of the RAC improved these values (Table 3.S10) and effectively corrected any issues of spatial autocorrelation (measured as Moran's I of the residuals) in all models except Australasia. The autocorrelation term was identified as a relevant variable in all models with importance ranging from 23.6% (global) to 57.1% (Nearctic. Table 3.2).

In the global BRT, the variable contributing most to explain differences in percentage of threatened mammals across grids was the type of biome in which they occur (38.1% importance. Table 3.2). Fixing the rest of indicators at their mean (partial dependency plots, PDP; Fig. 3.2A), we found the highest predicted percentage of threatened mammals occured in the Indomalay realm, followed by the Ecotone.

The Afrotropics, the Neotropics and Asia presented similar predicted values, while Europe and the Nearctic were predicted to have the lowest percentages of threatened mammals. A single land-use extent indicator, forest coverage, was identified as relevant globally, with a 7.2% importance (Fig. 3.2B), with higher proportions of threatened species occurring in less-forested areas (Figs. 3.S1 and 3.S9). No indicators of intensity or history were identified as relevant globally (Table 3.2).

Realm-specific BRTs offered an interesting picture with no unique group of land use indicators (land-use extent, intensity or history) consistently identified as most relevant. Different variables were identified as important for the distinct biogeographic realms (Table 3.2, Fig. 3.2). Indicators of land-use extent were relevant in Asia, Australasia, Europe, Indomalay, and the Neotropics; land-use intensity appeared as important in the Afrotropics, Europe, Indomalay and the Neotropics; while land-use history presented a relevant contribution only in the Indomalay realm. No land use indicator appears to explain threatened terrestrial mammals distribution in the Nearctic realm.

In relation to our second goal, our results provided support for both the *refuge* and the *threat* hypotheses, depending on the biome. The *refuge* hypothesis was supported by observed relationships within three biomes: Afrotropics, Australasia and

Table 3.2. Parameters and results of the BRTs, global and by realm. *Moran's I* was calculated for the residuals of each cell and the grid-cells surrounding it (queen neighbors; max.=8). *RAC,* residuals spatial autocovariate. Bold numbers indicate variables considered as relevant (i.e. their importance is greater than the expected under uniformity).

	Global	Afro.	Asia	Austr.	Europe	Indo.	Nearctic	Neotrop.
Tree complexity	10	10	10	10	10	10	10	10
Learning rate	0.050	0.001	0.001	0.001	0.001	0.001	0.001	0.001
Bag fraction	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50
No. trees	1550	8100	6150	3650	6150	5150	4800	4900
Residuals Moran's I	-0.04	-0.06	-0.04	0.12***	-0.06	-0.03	-0.03	-0.06
% Deviance explained	82.50	64.36	82.36	43.44	81.23	77.03	61.78	62.69
Variables (importance)								
Land-use extent								
Built-up	2.99	4.11	3.87	2.56	**7.33**	1.62	3.57	2.55
Cropland	2.17	4.30	2.65	4.87	1.48	1.54	4.63	6.40
Forest	**7.16**	2.87	**16.12**	**25.58**	**20.61**	**23.89**	3.84	**13.22**
Grazing land	2.56	5.60	2.50	5.08	1.67	1.91	2.94	6.66
No used	2.01	5.19	1.71	2.97	2.75	1.85	2.39	2.33
Land-use intensity								
Fertilizer	2.56	4.01	3.31	2.83	1.52	3.79	3.17	1.44
Irrigated area	2.08	2.07	1.48	3.53	**9.23**	3.93	2.46	2.11
Maize	2.78	4.18	1.48	3.22	2.98	2.11	2.75	**14.21**
Rice	5.43	**7.40**	5.11	0.93	5.87	3.63	0.00	1.25
Wheat	2.44	4.98	4.43	3.10	5.79	**13.22**	7.65	2.95
Oil palm	0.66	4.24	-	0.55	-	2.02	-	0.11
Soy	1.21	1.47	0.41	0.18	4.38	6.28	3.49	6.74
Land-use history								
TFU	4.00	5.78	5.08	4.83	5.56	**11.08**	6.04	1.85
Island	0.26	-	0.00	-	0.03	0.60	-	0.00
Realm	**38.12**	-	-	-	-	-	-	-
RAC	**23.57**	**43.80**	**51.84**	**39.77**	**30.79**	**22.53**	**57.07**	**38.16**

***p<0.001

Indomalay, where higher portions of threatened mammals occurred in areas where the extent and/or intensity of land use was relatively low. In particular, in the Afrotropics, the best predictor was rice yield (variable importance 7.40%), with areas with lower

yields associated with higher percentages of threatened mammals (Fig. 3.2). In Australasia, areas with more forest cover were associated with higher percentages of threatened mammals (variable importance 25.6%). This same relationship was observed within the Indomalay realm, where forest also had a high importance in the model (23.9%). In the Indomalay realm wheat yield (tones/ha) additionally appeared as relevant (variable importance 13.2%), with more threatened species in areas of lower intensity. Finally, TFU also appeared as relevant in this realm with different periods associated with higher percentages of threatened mammals (c.B.C.1000, c.A.D. 0, 1900 and 2000; Figs. 3.2 and 3.S14).

The *threat* hypothesis was supported by results from Asia and partly from Europe. The single relevant indicator in the Asia BRT was the percentage of forest per grid cell (variable importance 16.1%), with higher percentages of threatened species found in cells with less forest. In Europe, the other region within the Palearctic, forest (variable importance 20.6%), irrigated lands (9.2%) and built-up area (7.3%) were good predictors of the percentage of threatened mammals. As in Asia, more threatened species occurred in areas with lower forest cover, and also in intensively used —irrigated— lands. However, contrary to the prediction of the *threat* hypothesis, fewer threatened mammals were found in more built-up European areas.

Finally, results from the Neotropics offer support for both hypotheses. Relevant variables included maize yield (variable importance 14.2%) and forest area (13.2%), with more threatened mammals occurring in maize-intensive croplands (as expected from the *threat* hypothesis) and/or in areas with a greater cover of forest (as expected from the *refuge* hypothesis). These results may reflect the existence of heterogeneous and spatially segregated processes within this realm that should be explored with additional regional data.

Discussion

To our knowledge the present study is the first attempt to investigate the relative importance of different global land-use indicators and their influence on the distribution of threatened mammals, both globally and by biogeographic realm. Our

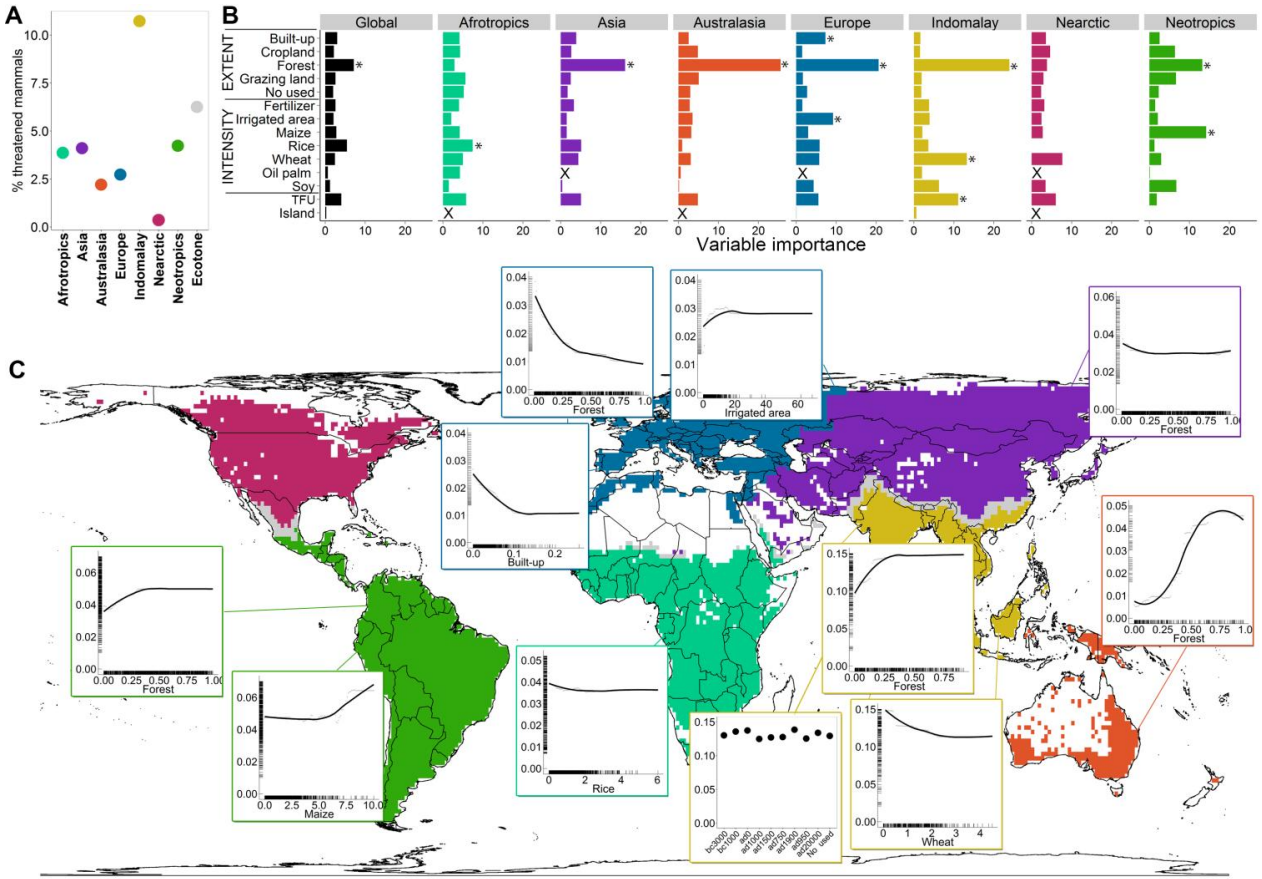


Figure 3.2. Results of the BRT including land use, intensity and history metrics. Y-axis represent % threatened mammals per grid-cell in all panels. *Panel A* presents the partial dependency plot (PDP) of the variable "realm" of the global BRT. *Panel B* shows the relative importance of each variable in the global (black) and region-based models (colored as in the map), with asterisks highlighting those with relevant contributions. Crosses indicate that the variable does not exist for that region. The addition of variables' importance does not sum 100% because the contribution of the spatial autocovariate is not shown, neither the contribution of the factor "realm" to the global model (see Table 2). *Panel C* shows the different regions for which models where fitted and PDPs of relevant variables for each (colored frame matching the regions').

first objective was to identify if any group of indicators could be defined as the most important contributor and we showed that, although our models explained the occurrence of threatened species well at both global and realm level, no single group clearly stood out above the others. Different metrics were important for different realms, highlighting the need to consider multiple indicators and to separate areas with different human and biodiversity histories when studying macroecological patterns of land use versus biodiversity. The second objective was to clarify their relationship with percentage of threatened mammals by comparing two proposed hypotheses: *refuge* and *threat*; we found evidence of both hypotheses in different realms and even simultaneously within a realm.

Our results identified forest as relevant in the global analyses and in five of the seven realm-specific models (Table 3.2) highlighting the importance of forested areas within agricultural lands. However, how forest associates with the percentage of threatened mammals varied regionally. In some regions, like Papua New Guinea (Fig. 3.S4) in Australasia, or Indonesia and Malaysia (Fig. 3.S6) in the Indomalay, the remaining large extensions of forest coincided with the highest richness of threatened terrestrial mammals (Amori et al. 2012; Rosauer & Jetz 2014), thus supporting the *refuge* hypothesis. These potential *refuge* areas are not exempt from threats including those derived from wood extraction and other agricultural activities (e.g. oil palm; Fitzherbert et al. 2008; Lenzen et al. 2012), but may still have the potential to preserve sensitive species. In other regions the pattern reversed, with co-occurrence of low forest surface and high number of threatened mammals. In Europe, less forest and more irrigated lands coincided with threatened mammals, which overall supported the *threat* hypothesis (Figs. 3.2 and 3.S5). Conversely, in Asia the lower coverage of forest may be a mixture of at least two opposite types of landscapes: lands with high level of endemism and therefore threatened species, like the Tibetan Plateau (Fig. 3.S3; Tang et al. 2006); or intensive croplands where species are more exposed to agricultural human pressures (likely rice and/or wheat crops; Fig. 3.S11); however there is not a clear preponderancy of any of them and that is why they do not appear as relevant in our models. Within the Neotropics higher percentages of threatened terrestrial mammals coincided with the great forested area of the Amazon, but also with the

Andean maize belt (Leff et al. 2004), a region containing recognized hotspots of endemism but also extensive agricultural lands (Brooks et al. 2002); thus supporting both *refuge* and *threat* hypotheses. In general, while forest was often identified as important, the relevance of other land use components, i.e. built-up area, cropland, grazing land and no-used area, was generally limited. The exception was built-up areas in Europe, where threatened mammals are nearly absent from highly urbanized areas (Fig. 3.2C).

Land-use intensity metrics normally appeared as secondary in importance after land-use extent indicators (Table 3.2) and the most relevant indicator varied from realm to realm: rice yield was relevant in the Afrotropics, irrigated land in Europe, wheat yield in the Indomalay and maize yield in the Neotropics. The relationships of these metrics with the percentage of threatened mammals supported the patterns found with land-use extent metrics in Europe and the Indomalay. Nevertheless, within the vast and diverse Neotropical realm, it was possible to find patterns consistent with the *refuge* hypothesis (pointed out by forest metric), coinciding with those areas of relatively halted natural-land clearance (Nepstad et al. 2009); but also with the *threat* hypothesis (indicated by maize-yield metric), likely overlapping with areas of rapid deforestation (Gasparri & Grau 2009).

We initially considered land-use history as a promising metric based on previously reported findings (Greuter 1994; Dullinger et al. 2013). However, in our study it was only identified as relevant in the Indomalay realm and the relationship was complex with areas first modified in c.B.C. 1000, c.A.D.0, 1900 and 2000 having higher proportions of threatened species (Fig. 3.2C). These heterogeneous patterns are difficult to interpret probably because time since first use is a too simplistic metric to capture the complexities of land use legacy. In some other regions, like Europe, which may have already suffered extinction filters (Balmford 1996; Turvey & Fritz 2011), most sensitive mammals are likely to have already disappeared, thus the proportion of currently threatened mammals would be independent from time since first use and more driven by relatively recent processes. Future work would be necessary to characterize land use legacy with more comprehensive metrics that would allow us to better evaluate how past land use influences current biodiversity patterns.

Some considerations should be taken into account when comparing our results with previous findings, particularly regarding scale, because land use metrics are strongly scale-dependent (Gilroy et al. 2014). We analyzed data at a coarse resolution (~1x1º) commonly used in macroecological studies (e.g. Cardillo et al. 2006). Given the quality of the species distribution data using a finer resolution would likely over-estimate occurrence (Hurlbert & Jetz 2007); however, as a result we aggregated information from quite heterogeneous landscapes. In an effort to limit the effect of aggregating heterogeneity we excluded grid-cells without croplands, to focus primarily on areas where our metrics of land-use intensity (crop-based) were relevant. However, some heterogeneity still remains. Another limitation of our study is the quality of the species' distribution data. IUCN geographic range data are often criticized because they are based on different methodologies and do not define the actual species occurrence but rather the extent of occurrence (Rondinini et al. 2011). As a result, we may have considered a species to be present in a location where it is not actually found (although this problem is minimized at the scale of our analyses as previously discussed). Similarly, species may be classified as threatened based on different criteria, which may not reflect threats associated with land use or habitat changes (González-Suárez et al. 2013). Nevertheless, because we are analyzing a wide range of species in diverse areas we think these localized errors are unlikely to affect our overall results.

While our two proposed hypotheses seem apparently contradictory, we propose they could simply reflect different temporal stages in the process of human appropration of the landscape. This temporal variation may be detectable across time for a given area but also spatially within a fixed temporal window if different regions in the world are at different stages of land use development, as suggested by our results. The effect of land use on number of threatened species may follow a complex non-linear relationship (Fig. 3.3). Initially we expected that expanding agricultural systems, such as those found in the Indomalay, Afrotropics and Neotropics (Grassini et al. 2013; Laurance et al. 2014), would predominantly fit the predictions of the *threat* hypothesis (Fig. 3.3 I), while persistently and intensively cropped regions such as Europe would fit the *refuge* hypothesis (Fig. 3.3 II). However, we found the opposite, which suggests we

are actually further along the land use development process than we anticipated (Corlett 2013). At this point, we have more "pristine" (but clearly already humanized) areas where we detect patterns consistent with the *refuge* hypothesis and what we describe as *'novel' threat* areas (Fig. 3.3 III) where the most sensitive species are long gone and continued development is now putting at risk species which were initially unaffected (Newbold et al. 2015).

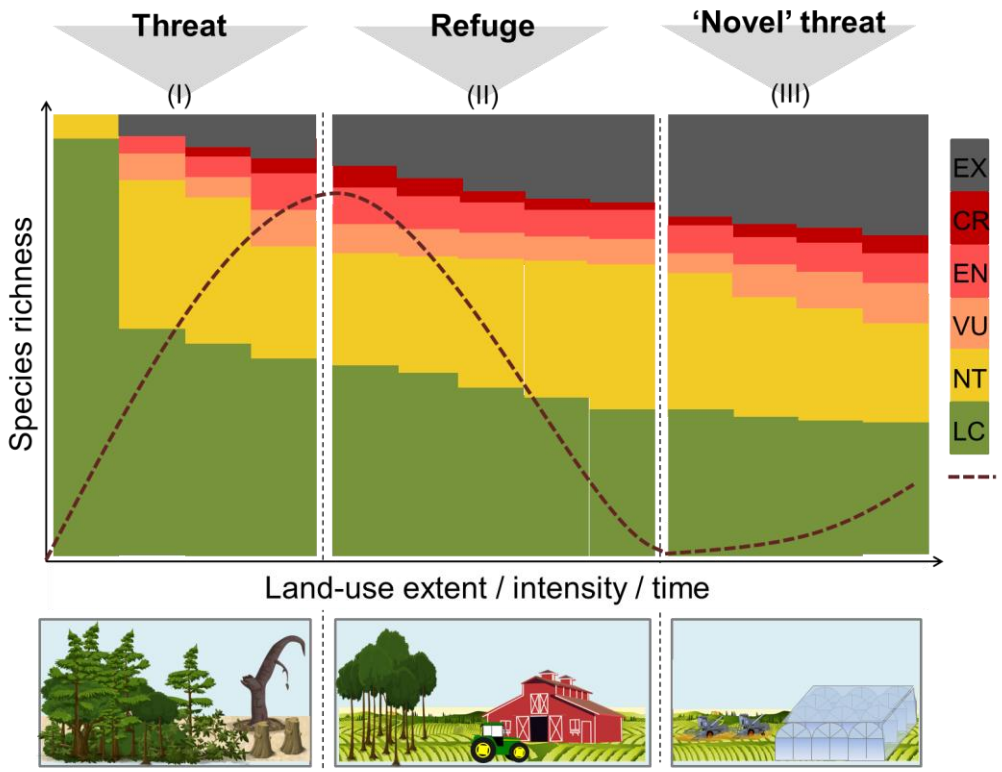


Figure 3.3. Summary of our proposed continuous hypothesis, adding '*novel' threat* areas (III), according to the obtained results. X axis represents land-use extent, intensity or time since first use within a certain area; Y axis represent total species richness. Legend: *EX,* extinct; *CR,* critically endangered; *EN,* endangered; *VU,* vulnerable; *NT*, near threatened; *LC,* least concern. *Thr,* number of threatened species. Species' categorization according to the IUCN Red List (IUCN 2014).

Although we found no evidence of what we may call genuine *threat* areas, which are expected to occur at the initial stages of land use development, it is likely that these may still exist in more localized areas and could be detected with analyses at finer scales (Sanderson et al. 2002). Nevertheless, many of these remaining pristine

regions are areas with low primary productivity, which results in limited human exploitation but also low species richness (Davies et al. 2007; Luck 2007), thus these areas are unlikely to preserve mammals as a whole. Our analyses suggest that at a large scale no areas can still be considered as in early stages of land use development. As human land use expands and intensifies we are moving along dampening cycles, losing biodiversity and impoverishing the mammalian fauna worldwide (Fig. 3.3).

Previous global studies have mainly reported results consistent with the *threat* hypothesis around the world, relating proxies of human impact (e.g. population density, land-use metrics) to threatening effects on mammals and other species (Mcpherson & Nieswiadomy 2005; Lenzen et al. 2009). Our contrasting results are likely consequence of the study unit —most similar studies use country level data, whereas we employed grid cells. Furthermore, many global studies do not separate regions with different human histories (e.g. McKee et al. 2003), potentially missing interesting and contrasting patterns as we show here.

This study provides a first global perspective of the complex effects of land use development stage for mammalian biodiversity which can help us better understand the potential consequences of future land use changes. Areas where most of the future agricultural expansion is predicted to occur show patterns consistent with the *refuge* hypothesis, with vulnerable species remaining in areas that may be soon further transformed, leading to considerable biodiversity losses (Grassini et al. 2013; Laurance et al. 2014). Potential conservation actions to protect mammalian fauna in *refuge* areas would require the limitation of land use expansion into natural areas and a careful planning of further intensification. On the other hand, within the *'novel' threat* areas, any remaining threatened species must survive in a highly modified environment, however, there is some hope derived from socioeconomic changes within these regions, e.g. farmland abandonment, that could bring their partial recovery (Navarro & Pereira 2012; Boitani & Linnell 2015).

Acknowledgements

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Supporting Information

Appendix 3.S1. Supplementary data description

Table 3.S1. Indicators of land-use extent, intensity and history. Short name is used in the main manuscript.

Indicators						
Long name	*Short name*	Units	Year	Original resolution	Data sources	Reference
Land-use extent						
Urban and infrastructure	Built-up	% grid cell	2000	5 min	Eurostat, national inventories, GLC2000	Erb et al. (2007)
Cropland	Cropland	% grid cell	2000	5 min	Ramankutty & Foley (1999), FAO	Erb et al. (2007)
Forest	Forest	% grid cell	2000	5 min	FRA2000, GLC2000	Erb et al. (2007)
Grazing land	Grazing land	% grid cell	2000	5 min	GLC2000	Erb et al. (2007)
Areas without land use	No used	% grid cell	2000	5 min	Human footprint (Sanderson et al. 2002), GLC 2000	Erb et al. (2007)
Land-use intensity						
Inputs						
Industrial and manure fertilizer application rates (N, P)	Fertilizer	kg/ha	2000	10 km	FAO "Fertilizer Use by Crop 2002" combined with harvested area for 175 crops (Monfreda et al. 2008).	Potter et al. (2010)
Land equipped for irrigation	Irrigated area	% grid cell	2000	5 min	FAO, World Bank and other international organizations, USGC-GLCC-2.0 and JRC-GLC2000	Siebert et al. (2015)
Outputs						

Indicators						
Long name	*Short name*	Units	Year	Original resolution	Data sources	Reference
Yields for rice, wheat and maize	Maize, rice and wheat	tons/ha	2000	5 min	Combining census statistics with global cropland area (Ramankutty et al. 2008)	Monfreda et al. (2008)
Harvested area for soy and oil palm	Soy and oil palm	% grid cell	2000	5 min	Combining census statistics with global cropland area (Ramankutty et al. 2008)	Monfreda et al. (2008)
Land-use history						
Time period of first significant land use[1]	TFU	year (category)	-	5 min	KK10 model (Kaplan et al. 2011)	Ellis et al. (2013)

[1] Categories: BC6000, BC3000, BC1000, AD0, AD1000, AD1500, AD1750, AD1900, AD1950, AD2000, No used.

Correlation among variables

Table 3.S2. Spearman's rank coefficient of correlation (ρ) for all pairs of variables included in the global BRT.

	Mammal richness	Threatened mammals	Built-up	Cropland	Forest	Grazing land	No used	Irrigated area	Fertilizer	Wheat yield	Maize yield	Rice yield	Oil palm
Threatened mammals	0.64												
Built-up	-0.15	-0.15											
Cropland	-0.09	0.01	0.67										
Forest	0.39	0.22	-0.14	-0.23									
Grazing land	-0.11	-0.09	-0.16	-0.17	-0.61								
No used	-0.24	-0.14	-0.25	-0.34	-0.24	-0.37							
Irrigated area	-0.11	0.02	0.29	0.52	-0.21	-0.04	-0.13						
Fertilizer	-0.12	-0.02	0.54	0.62	-0.19	-0.09	-0.18	0.66					
Wheat yield	-0.12	-0.14	0.53	0.42	-0.20	0.11	-0.27	0.32	0.52				
Maize yield	-0.07	-0.08	0.52	0.47	-0.16	0.06	-0.29	0.25	0.48	0.61			
Rice yield	0.18	0.31	0.10	0.31	-0.06	0.06	-0.24	0.36	0.38	0.25	0.33		
Oil palm	0.10	0.22	-0.02	0.06	0.02	-0.03	-0.04	-0.02	0.00	-0.06	0.00	0.05	
Soy	-0.04	-0.05	0.28	0.31	-0.10	-0.04	-0.10	0.10	0.31	0.21	0.35	0.10	0.00

Table 3.S3. Spearman's rank coefficient of correlation (ρ) for all pairs of variables included in the Australasia BRT.

	Mammal richness	Threatened mammals	Built-up	Cropland	Forest	Grazing land	No used	Irrigated area	Fertilizer	Wheat yield	Maize yield	Rice yield	Oil palm
Threatened mammals	0.76												
Built-up	-0.04	0.01											
Cropland	-0.19	-0.21	0.64										
Forest	0.74	0.68	-0.07	-0.28									
Grazing land	-0.44	-0.46	-0.11	-0.03	-0.57								
No used	-0.30	-0.20	-0.32	-0.40	-0.42	-0.24							
Irrigated area	-0.04	-0.07	0.26	0.40	-0.11	0.00	-0.18						
Fertilizer	-0.12	-0.10	0.42	0.75	-0.15	-0.03	-0.36	0.17					
Wheat yield	-0.14	-0.20	0.61	0.83	-0.18	-0.04	-0.38	0.41	0.68				
Maize yield	0.37	0.22	0.42	0.54	0.21	-0.25	-0.42	0.43	0.38	0.67			
Rice yield	0.23	0.19	0.34	0.42	0.20	-0.28	-0.29	0.57	0.18	0.36	0.57		
Oil palm	0.55	0.46	-0.10	-0.18	0.53	-0.31	-0.20	-0.09	-0.09	-0.24	0.18	0.22	
Soy	0.14	0.20	0.14	0.12	0.11	-0.04	-0.18	0.25	0.26	0.19	0.19	0.19	-0.06

Table 3.S4. Spearman's rank coefficient of correlation (ρ) for all pairs of variables included in the Afrotropics BRT.

	Mammal richness	Threatened mammals	Built-up	Cropland	Forest	Grazing land	No used	Irrigated area	Fertilizer	Wheat yield	Maize yield	Rice yield	Oil palm
Threatened mammals	0.59												
Built-up	0.08	0.07											
Cropland	0.18	0.07	0.45										
Forest	0.50	0.20	-0.14	-0.21									
Grazing land	-0.46	-0.21	-0.05	-0.16	-0.78								
No used	-0.22	-0.05	-0.11	-0.19	-0.21	-0.27							
Irrigated area	-0.09	-0.07	0.19	0.11	-0.13	0.08	-0.03						
Fertilizer	0.05	0.01	0.61	0.27	-0.15	0.04	-0.07	0.09					
Wheat yield	0.05	-0.04	0.13	0.04	-0.08	0.12	-0.11	0.05	0.23				
Maize yield	0.10	-0.02	0.45	0.33	-0.25	0.17	-0.16	0.13	0.39	0.25			
Rice yield	0.09	0.00	0.22	0.28	-0.15	0.13	-0.20	0.08	0.28	0.10	0.48		
Oil palm	0.05	0.06	0.01	0.19	0.00	-0.07	-0.03	-0.01	0.09	-0.08	0.05	0.05	
Soy	0.09	-0.02	0.11	0.35	-0.06	-0.07	-0.06	0.00	0.21	0.04	0.13	0.09	0.55

Table 3.S5. Spearman's rank coefficient of correlation (ρ) for all pairs of variables included in the Indomalay BRT.

	Mammal richness	Threatened mammals	Built-up	Cropland	Forest	Grazing land	No used	Irrigated area	Fertilizer	Wheat yield	Maize yield	Rice yield	Oil palm
Threatened mammals	0.89												
Built-up	-0.54												
Cropland	-0.63	-0.58	0.78										
Forest	0.63	0.68	-0.59	-0.75									
Grazing land	0.17	0.02	-0.39	-0.47	-0.18								
No used	-0.15	-0.14	-0.10	-0.13	-0.13	0.01							
Irrigated area	-0.51	-0.52	0.60	0.70	-0.58	-0.29	0.01						
Fertilizer	-0.39	-0.44	0.61	0.57	-0.50	-0.20	-0.04	0.76					
Wheat yield	-0.58	-0.65	0.47	0.51	-0.45	-0.18	0.05	0.63	0.51				
Maize yield	0.35	0.20	-0.11	-0.10	0.05	0.14	-0.15	-0.13	0.06	-0.35			
Rice yield	0.09	0.01	0.14	0.03	0.05	-0.09	-0.12	0.09	0.30	-0.06	0.45		
Oil palm	0.34	0.46	-0.18	-0.10	0.16	-0.05	-0.01	-0.18	-0.10	-0.30	0.14	0.00	
Soy	-0.16	-0.17	0.15	0.23	-0.14	-0.16	-0.04	0.10	-0.01	0.15	-0.07	-0.18	-0.07

Table 3.S6. Spearman's rank coefficient of correlation (ρ) for all pairs of variables included in the Nearctic BRT.

	Mammal richness	Threatened mammals	Built-up	Cropland	Forest	Grazing land	No used	Irrigated area	Fertilizer	Wheat yield	Maize yield	Rice yield
Threatened mammals	0.13											
Built-up	-0.16	0.07										
Cropland	-0.17	0.00	0.88									
Forest	0.00	-0.04	-0.31	-0.39								
Grazing land	0.61	0.12	-0.12	-0.11	-0.52							
No used	-0.50	-0.10	-0.39	-0.40	-0.15	-0.42						
Irrigated area	0.20	0.08	0.17	0.20	-0.20	0.20	-0.19					
Fertilizer	-0.12	0.00	0.75	0.85	-0.42	-0.04	-0.30	0.33				
Wheat yield	0.33	0.21	0.46	0.43	-0.26	0.34	-0.51	0.35	0.43			
Maize yield	0.14	0.09	0.58	0.60	-0.35	0.30	-0.51	0.38	0.61	0.63		
Rice yield	0.00	0.06	0.16	0.14	0.00	-0.04	-0.09	0.52	0.15	0.12	0.17	
Soy	-0.14	0.12	0.62	0.66	-0.26	-0.14	-0.18	0.16	0.78	0.35	0.45	0.18

Table 3.S7. Spearman's rank coefficient of correlation (ρ) for all pairs of variables included in the Neotropics BRT.

	Mammal richness	Threatened mammals	Built-up	Cropland	Forest	Grazing land	No used	Irrigated area	Fertilizer	Wheat yield	Maize yield	Rice yield	Oil palm
Threatened mammals	0.85												
Built-up	0.01	0.04											
Cropland	-0.29	-0.27	0.48										
Forest	0.61	0.54	-0.14	-0.26									
Grazing land	-0.64	-0.55	0.14	0.19	-0.80								
No used	0.24	0.17	-0.25	-0.38	-0.09	-0.45							
Irrigated area	-0.16	-0.10	0.32	0.22	-0.17	0.20	-0.16						
Fertilizer	-0.05	-0.10	0.33	0.48	-0.16	0.16	-0.24	0.39					
Wheat yield	-0.36	-0.32	0.18	0.34	-0.31	0.35	-0.25	0.34	0.39				
Maize yield	-0.50	-0.43	0.16	0.35	-0.39	0.36	-0.15	0.20	0.31	0.63			
Rice yield	-0.04	-0.02	0.24	0.24	-0.21	0.32	-0.30	0.33	0.37	0.38	0.31		
Oil palm	0.16	0.21	0.28	0.13	0.01	0.01	-0.09	0.22	0.31	0.03	-0.02	0.20	
Soy	-0.21	-0.25	0.04	0.27	-0.19	0.17	-0.12	0.00	0.38	0.38	0.39	0.21	-0.04

Table 3.S8. Spearman's rank coefficient of correlation (ρ) for all pairs of variables included in the Asia BRT.

	Mammal richness	Threatened mammals	Built-up	Cropland	Forest	Grazing land	No used	Irrigated area	Fertilizer	Wheat yield	Maize yield	Rice yield
Threatened mammals	0.66											
Built-up	0.27	-0.01										
Cropland	0.35	0.07	0.72									
Forest	0.12	-0.22	0.03	-0.08								
Grazing land	0.18	0.30	-0.05	0.00	-0.61							
No used	-0.49	-0.14	-0.34	-0.40	-0.26	-0.50						
Irrigated area	0.12	0.06	0.46	0.58	-0.19	0.13	-0.23					
Fertilizer	0.19	0.06	0.44	0.69	-0.14	0.03	-0.23	0.81				
Wheat yield	0.33	0.34	0.39	0.52	-0.22	0.23	-0.28	0.57	0.61			
Maize yield	0.41	0.31	0.45	0.62	-0.16	0.17	-0.32	0.52	0.55	0.79		
Rice yield	0.43	0.34	0.42	0.61	-0.09	0.07	-0.27	0.52	0.62	0.75	0.82	
Soy	0.20	0.07	0.29	0.54	-0.05	0.00	-0.21	0.49	0.72	0.48	0.53	0.57

Table 3.S9. Spearman's rank coefficient of correlation (ρ) for all pairs of variables included in the Europe BRT.

	Mammal richness	Threatened mammals	Built-up	Cropland	Forest	Grazing land	No used	Irrigated area	Fertilizer	Wheat yield	Maize yield	Rice yield
Threatened mammals	0.26											
Built-up	0.36	-0.21										
Cropland	0.53	0.10	0.57									
Forest	-0.01	-0.44	-0.14	-0.29								
Grazing land	0.04	0.34	-0.13	-0.15	-0.55							
No used	-0.52	0.10	-0.33	-0.44	-0.30	-0.25						
Irrigated area	0.26	0.28	0.25	0.35	-0.26	0.07	-0.10					
Fertilizer	0.20	-0.09	0.64	0.43	-0.18	-0.05	-0.20	0.41				
Wheat yield	0.41	-0.15	0.79	0.55	-0.15	-0.07	-0.33	0.25	0.83			
Maize yield	0.48	0.04	0.58	0.54	-0.13	-0.06	-0.32	0.36	0.72	0.71		
Rice yield	0.18	0.26	0.13	0.38	-0.20	0.04	-0.15	0.47	0.18	0.11	0.45	
Soy	0.30	0.05	0.25	0.23	-0.05	-0.06	-0.11	0.32	0.18	0.20	0.22	0.14

Maps of proportion of threatened mammals and relevant indicators globally, and by biogeographic realm

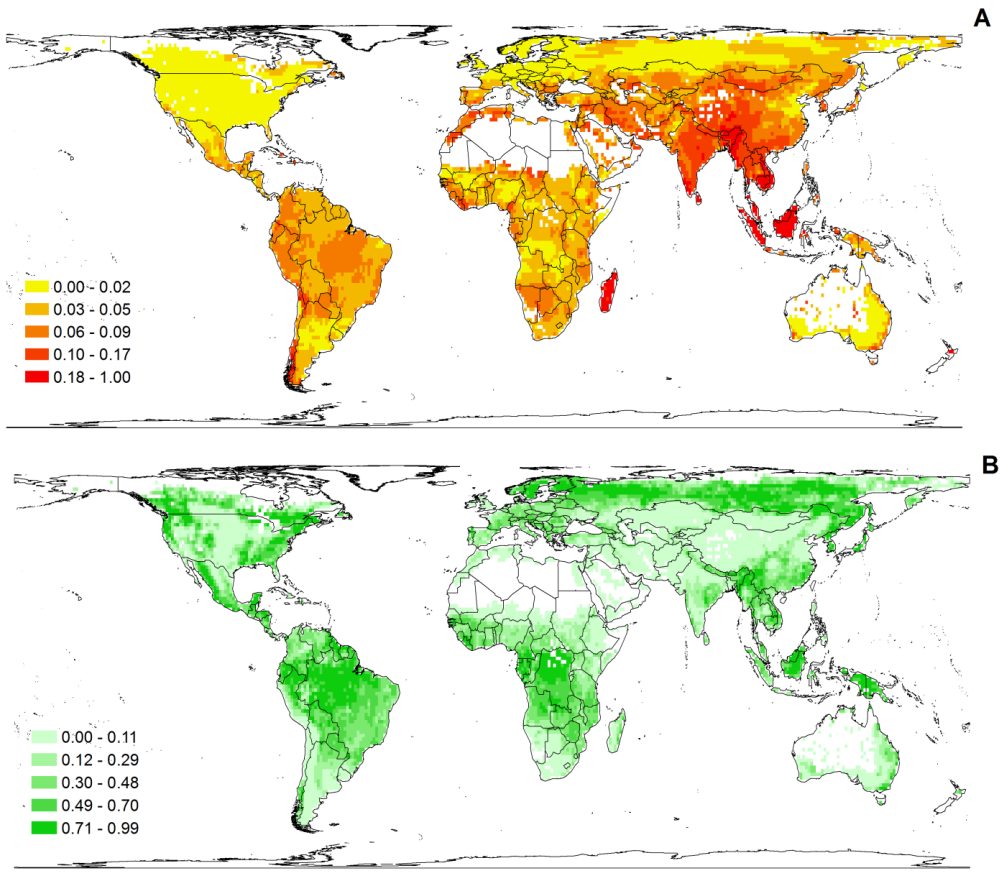


Figure 3.S1. Percentage of threatened mammals (A) and and percentage of forested area per grid cell (tons/ha; B).

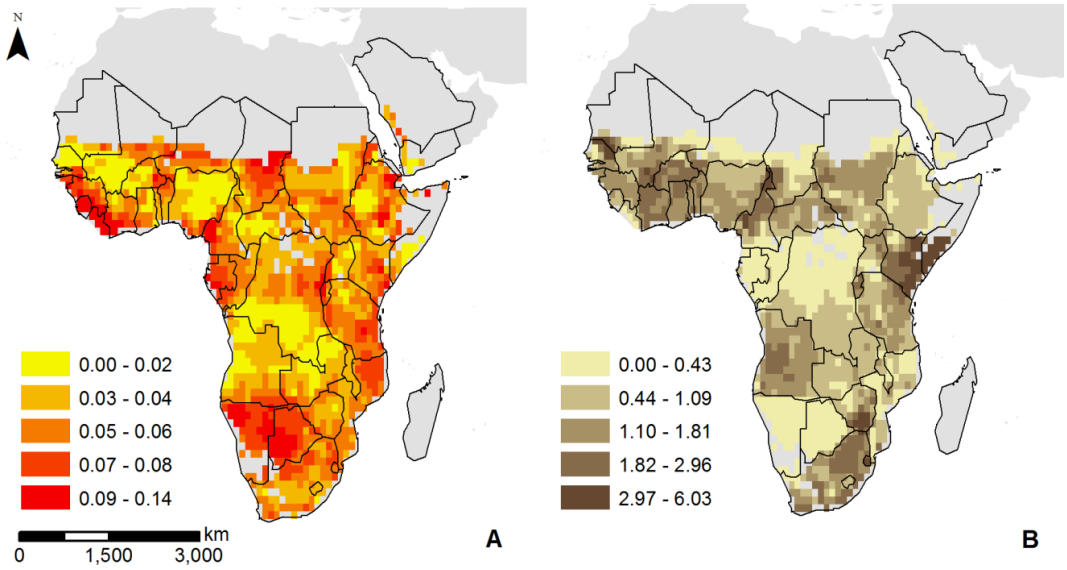


Figure 3.S2. Percentage of threatened mammals (A) and average rice yields per grid cell (tons/ha; B) in the Afrotropics realm.

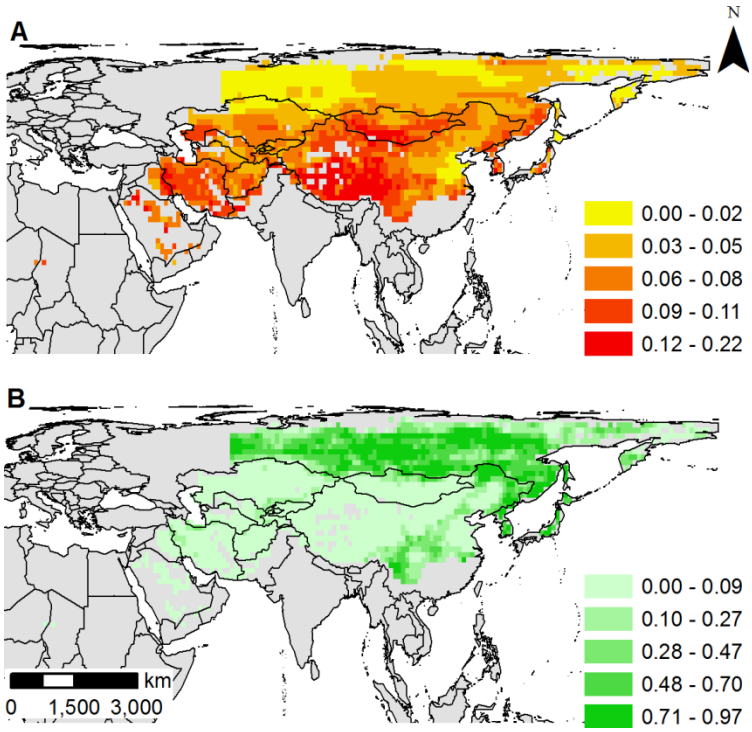


Figure 3.S3. Percentage of threatened mammals (A) and percentage of forested area per grid cell (B) in the Asia region (Palearctic realm).

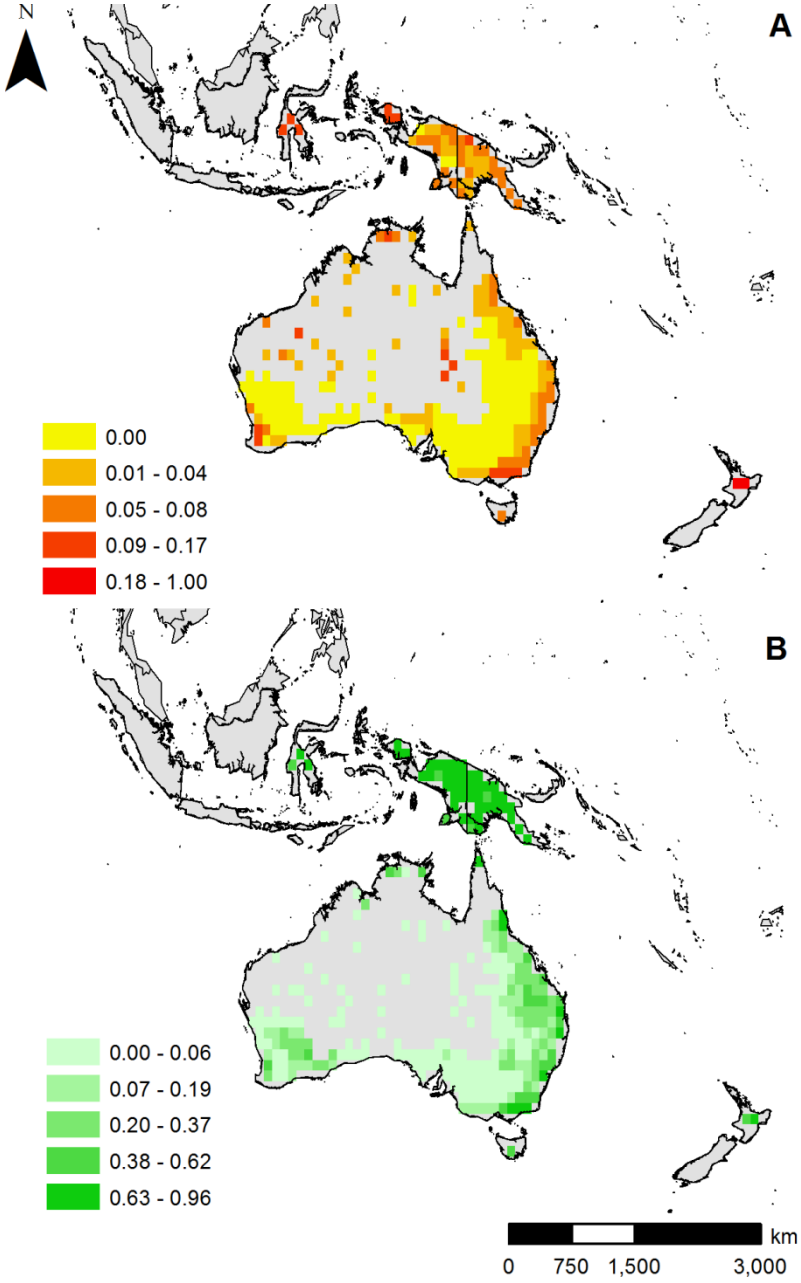


Figure 3.S4. Percentage of threatened mammals (A) and forested area per grid cell (B) in the Australasia realm.

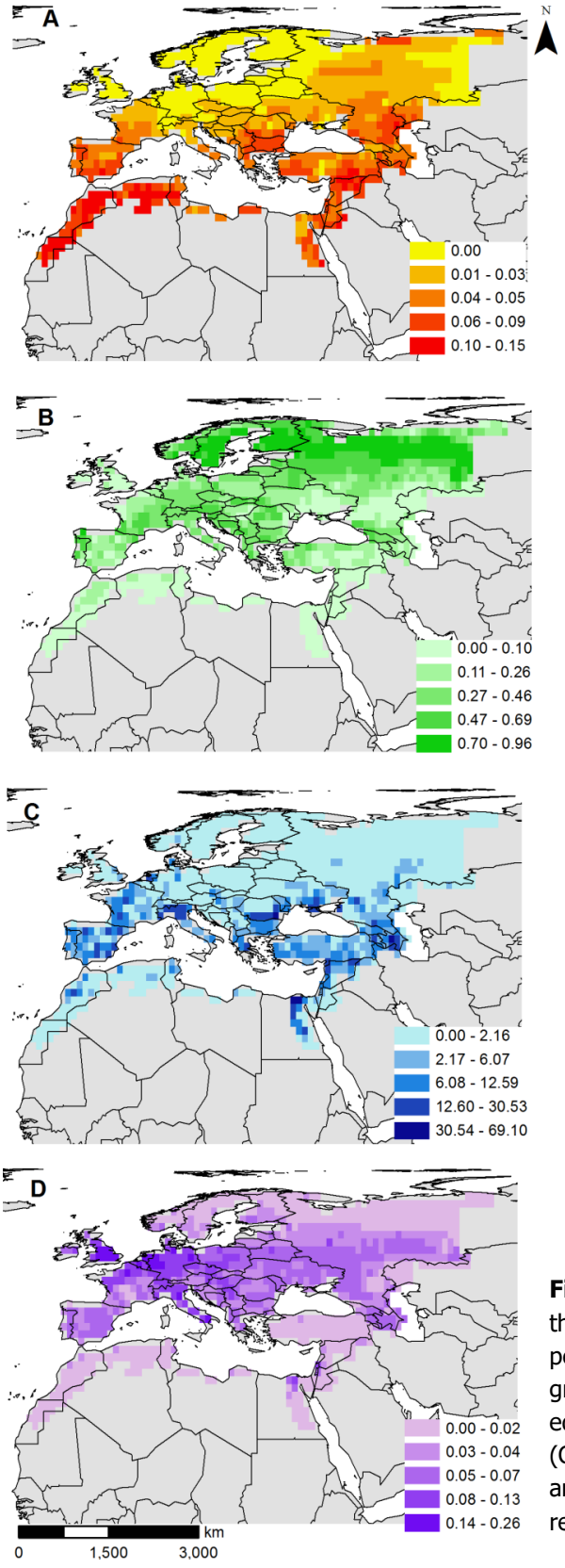


Figure 3.S5. Percentage of threatened mammals (A), percentage of forested area per grid cell (B), percentage of land equipped for irrigation per grid cell (C) and percentage of built-up area per grid cell(D) in the Europe region (Palearctic realm).

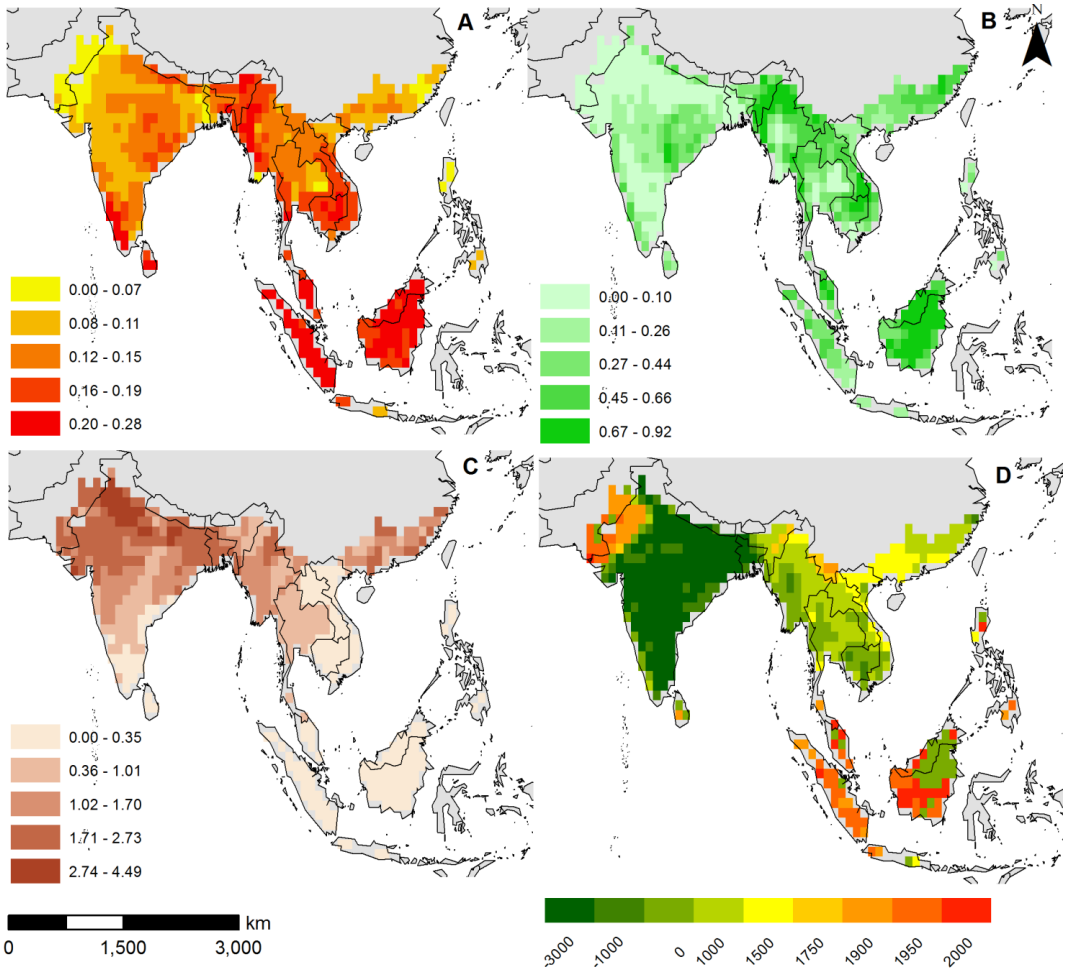


Figure 3.S6. Percentage of threatened mammals (A), forested area (B), average wheat yields per grid cell (tons/ha; C) and TFU (D) in the Indomalay realm.

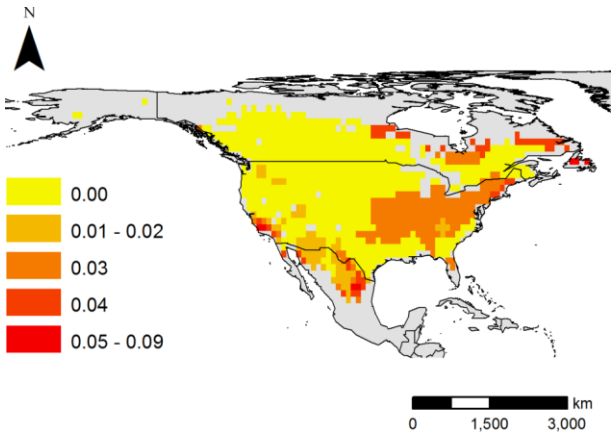


Figure 3.S7. Percentage of threatened mammals in the Nearctic realm.

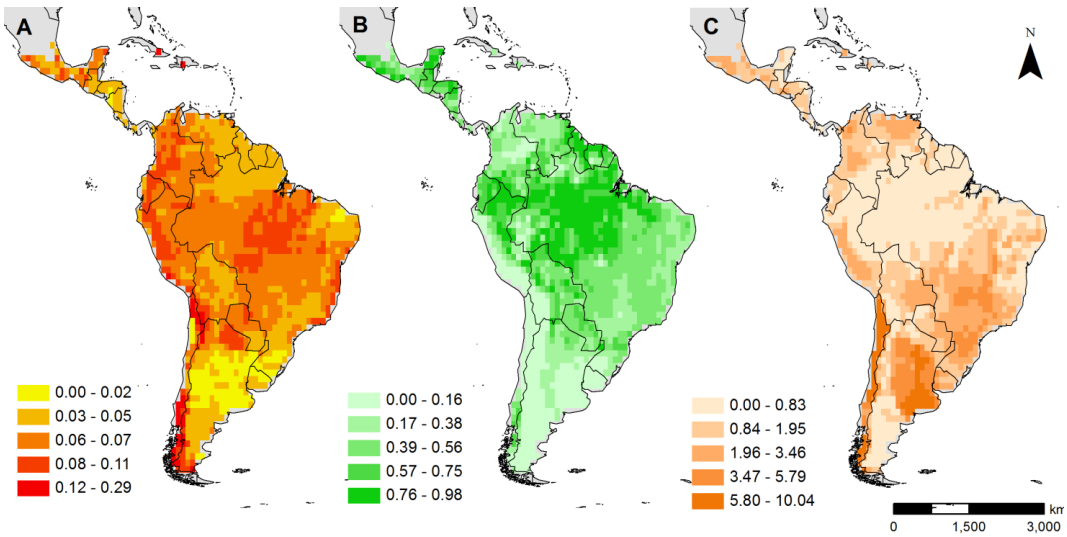


Figure 3.S8. Percentage of threatened mammals (A), forested area per grid cell (B) and maize yields (tons/ha; C) in the Neotropics realm.

Appendix 3.S2. Supplementary results: boosted regression trees

Global:

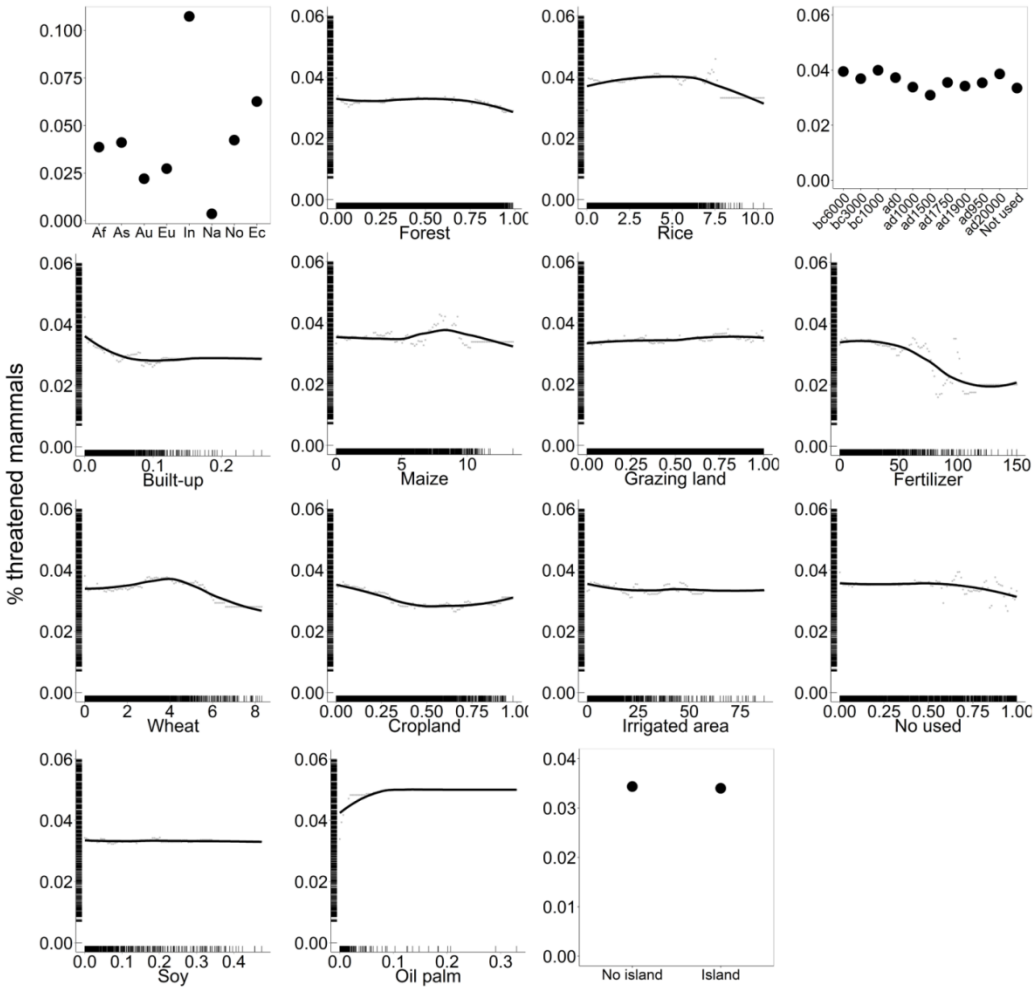


Figure 3.S9. Partial dependence plots (PDPs) of all variables included in the global BRT. Individual plots are ordered according to their relative importance in the BRT (Table 3.1, main manuscript).

Afrotropics:

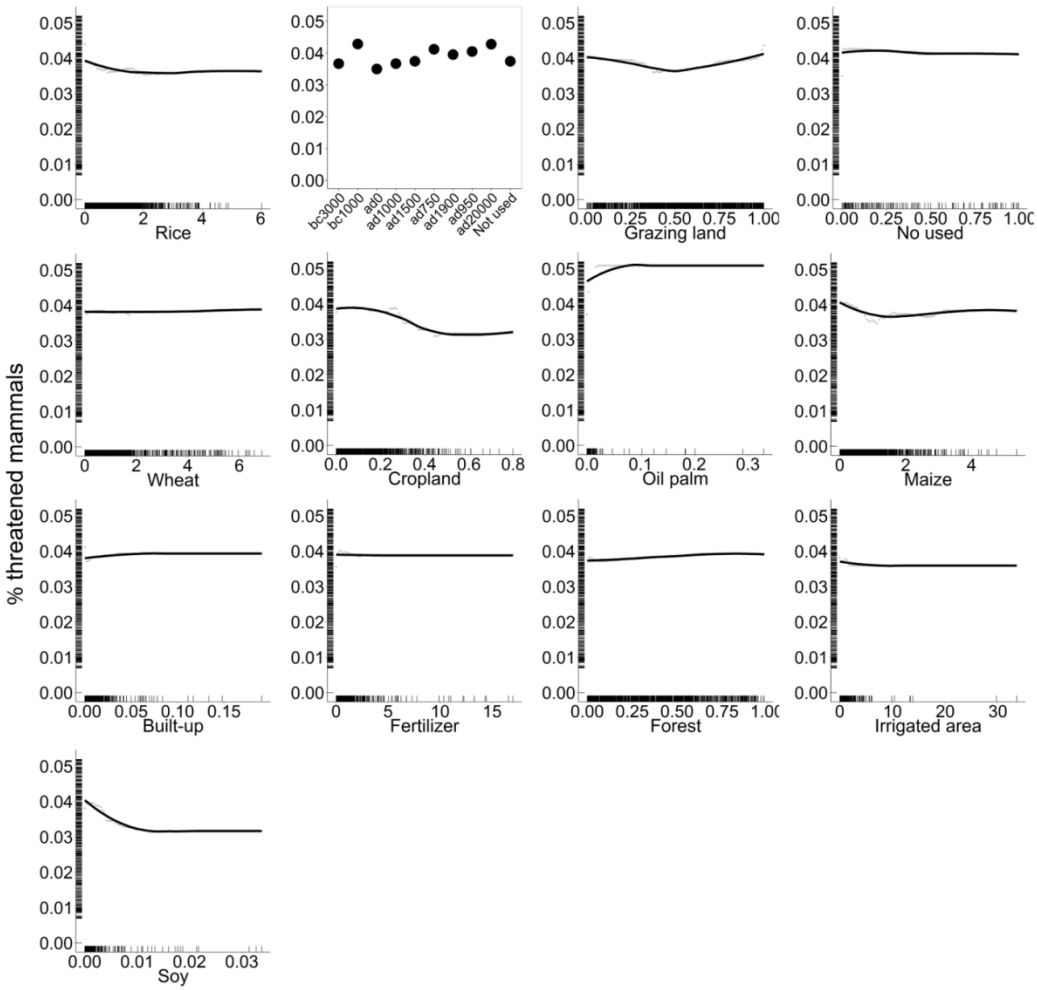


Figure 3.S10. Partial dependence plots (PDPs) of all variables included in the Afrotropics BRT. Individual plots are ordered according to their relative importance in the BRT (Table 3.1, main manuscript).

Asia (Palearctic):

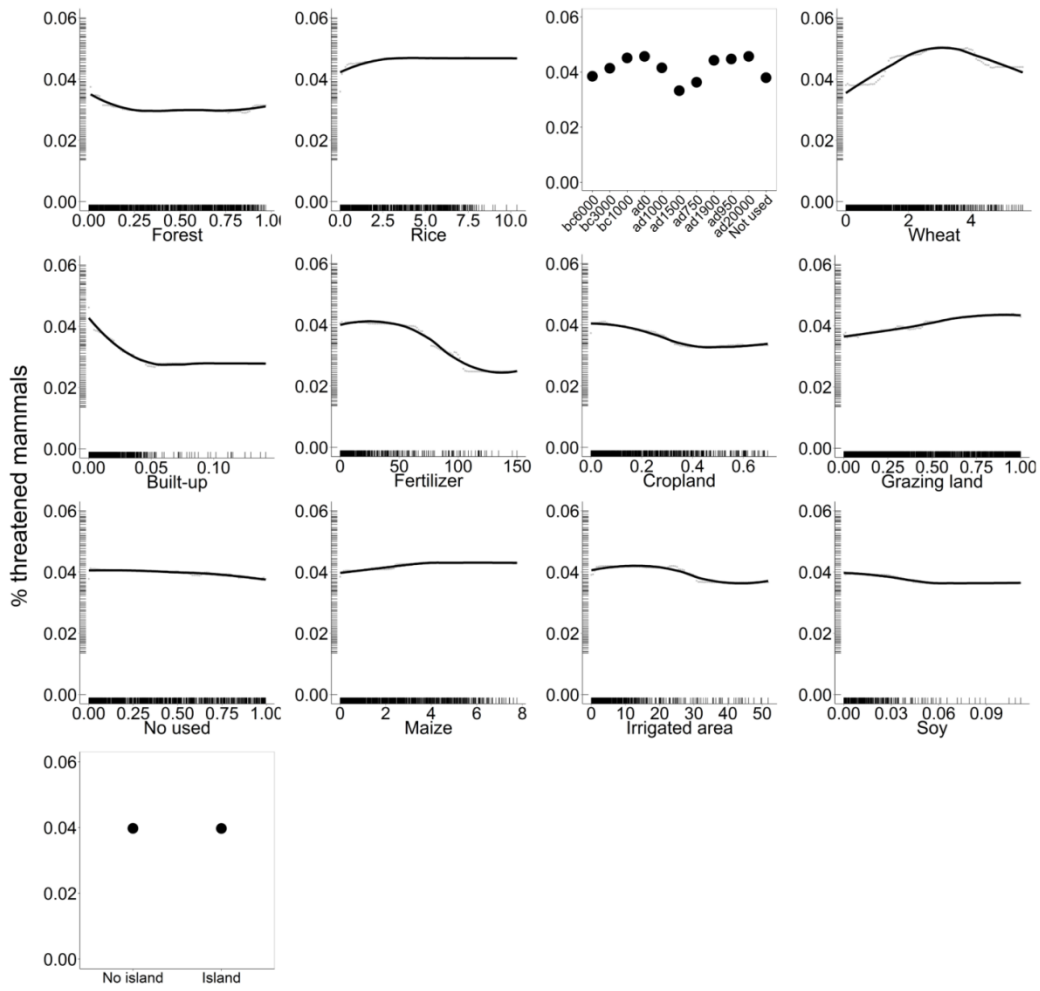


Figure 3.S11. Partial dependence plots (PDPs) of all variables included in the Asia BRT. Individual plots are ordered according to their relative importance in the BRT (Table 3.1, main manuscript).

Australasia:

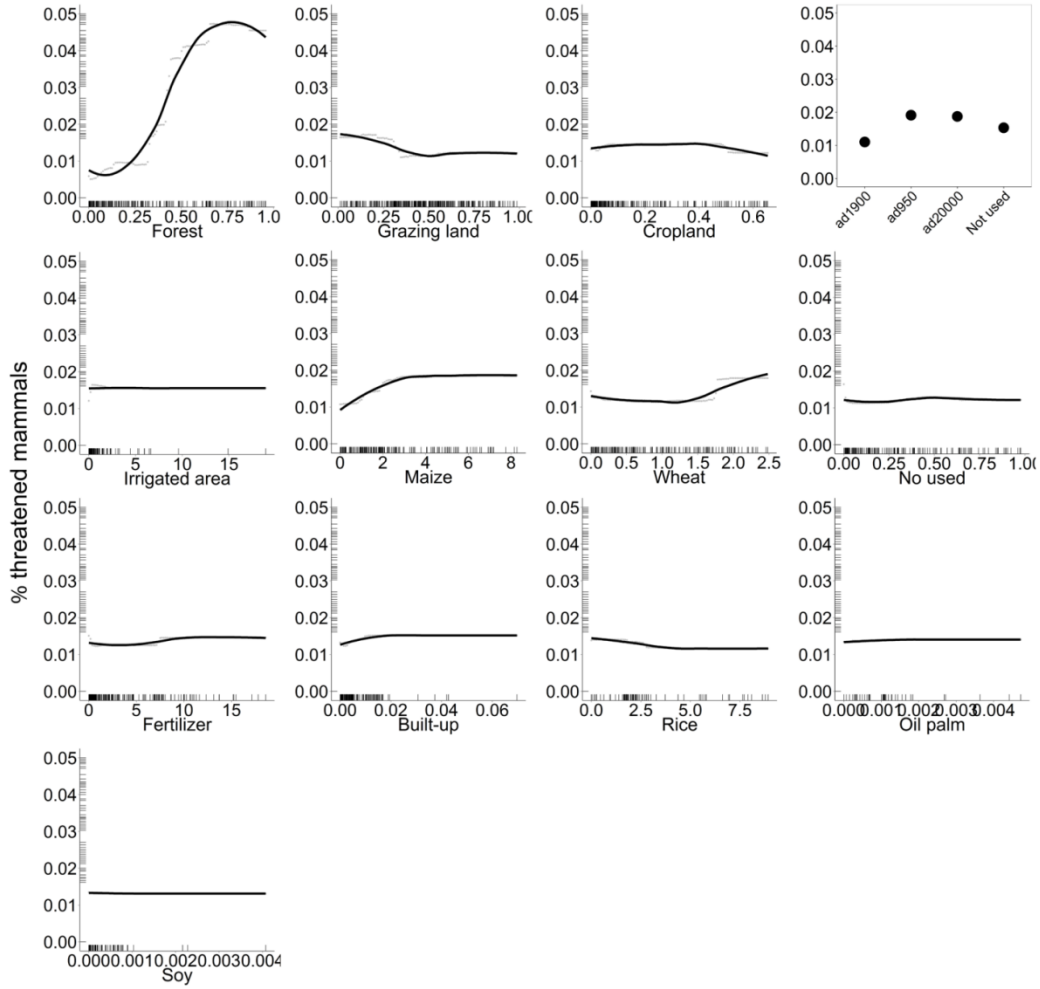


Figure 3.S12. Partial dependence plots (PDPs) of all variables included in the Australasia BRT. Individual plots are ordered according to their relative importance in the BRT (Table 3.1, main manuscript).

Europe (Palearctic):

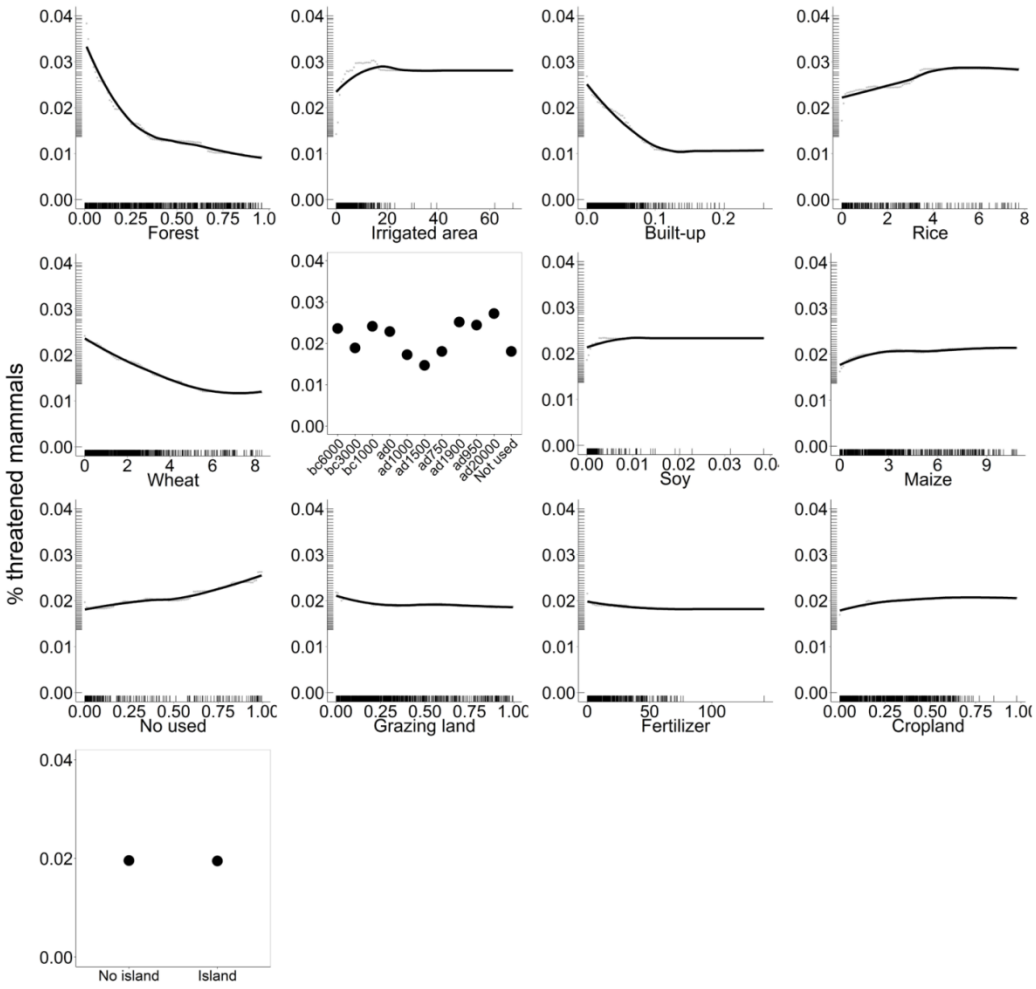


Figure 3.S13. Partial dependence plots (PDPs) of all variables included in the Europe BRT. Individual plots are ordered according to their relative importance in the BRT (Table 3.1, main manuscript).

Indomalay:

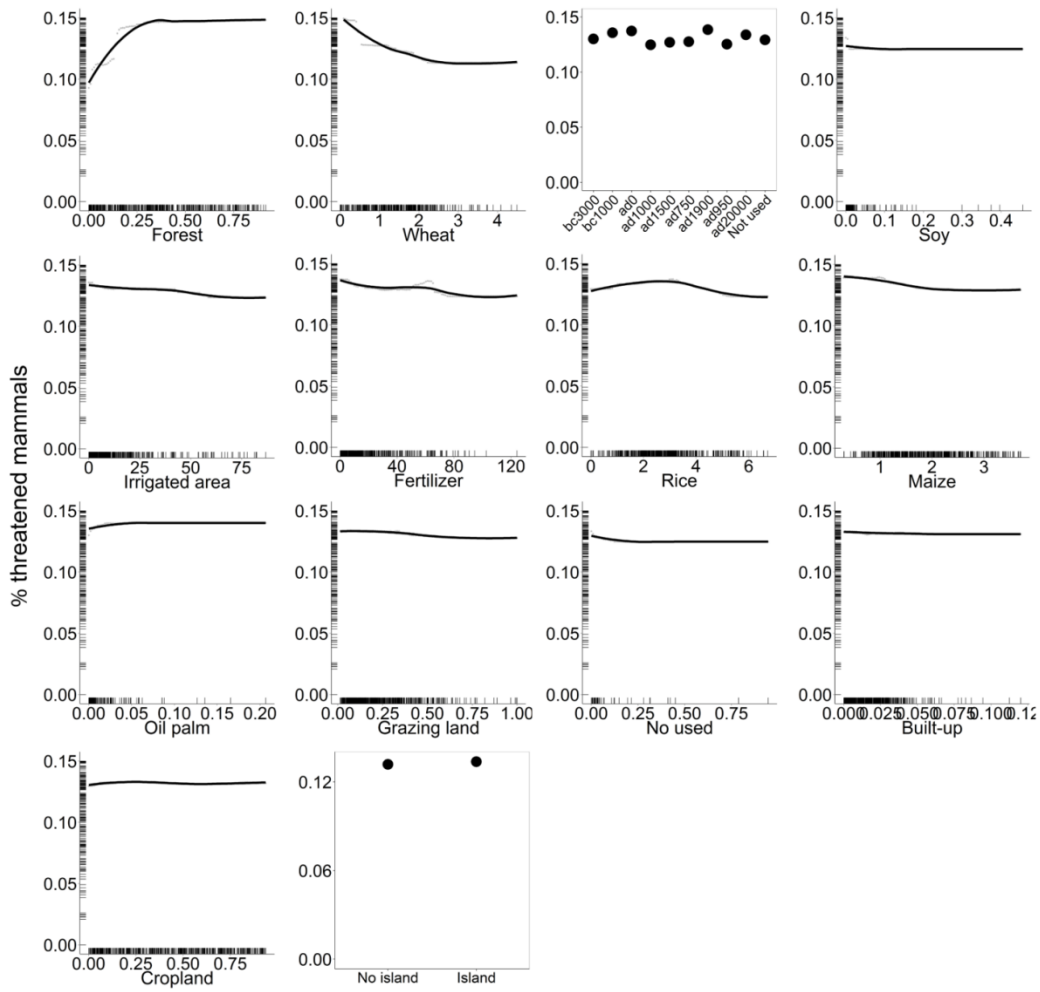


Figure 3.S14. Partial dependence plots (PDPs) of all variables included in the Indomalay BRT. Individual plots are ordered according to their relative importance in the BRT (Table 3.1, main manuscript).

Nearctic:

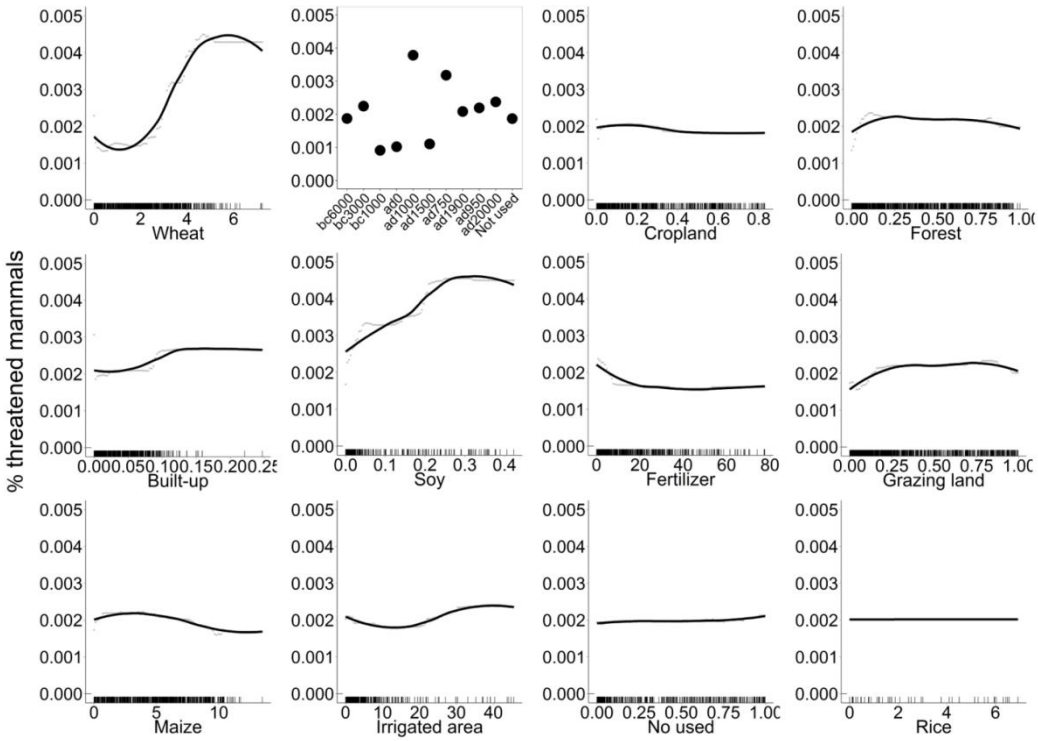


Figure 3.S15. Partial dependence plots (PDPs) of all variables included in the Nearctic BRT. Individual plots are ordered according to their relative importance in the BRT (Table 3.1, main manuscript).

Neotropics:

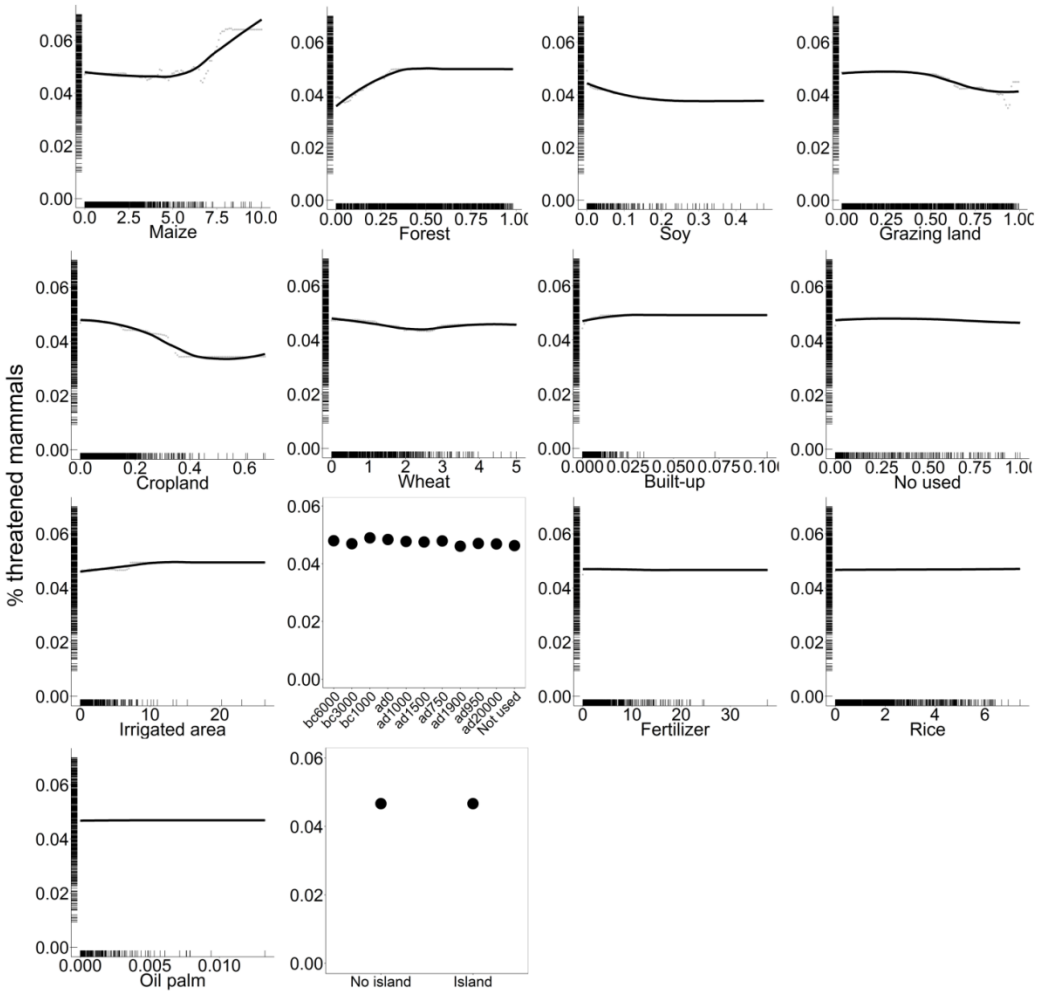


Figure 3.S16. Partial dependence plots (PDPs) of all variables included in the global BRT. Individual plots are ordered according to their relative importance in the BRT (Table 3.1, main manuscript).

Table 3.S10. Parameters and results of the BRTs, global and by realm, without including the residual autocovariate (RAC). *Moran's I* was calculated for the residuals of each cell and the grid-cells surrounding it (queen neighbors; max.=8). Bold numbers indicate variables considered as relevant (i.e. their importance is greater than the expected under uniformity).

	Global	Afro.	Asia	Austr.	Europe	Indo.	Nearctic	Neotrop.
Tree complexity	10	10	10	10	10	10	10	10
Learning rate	0.050	0.001	0.001	0.001	0.001	0.001	0.001	0.001
Bag fraction	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50
Number of trees	1900	11800	8700	2700	6650	6600	10050	6400
Moran's I	0.33***	0.29***	0.49***	0.19***	0.34***	0.21***	0.27***	0.38***
% Deviance explained	72.43	47.03	61.44	34.11	70.91	69.50	42.32	43.70
Variables (importance)								
LU extent								
Built-up	5.53	6.14	**8.93**	4.85	**9.89**	2.09	**11.57**	6.70
Cropland	5.13	**7.83**	5.98	**8.77**	2.97	2.71	**13.18**	6.56
Forest	**9.80**	5.02	**27.41**	**37.87**	**24.38**	**26.12**	7.41	**17.46**
Grazing land	5.39	**8.13**	7.48	**10.73**	4.89	3.84	**8.40**	**10.08**
No used	4.82	**8.31**	5.52	4.54	5.27	4.40	7.72	4.90
LU intensity								
Fertilizer	4.50	**8.43**	5.81	**9.29**	2.17	6.43	**8.90**	3.54
Irrigated area	4.31	5.26	4.02	7.39	**16.66**	5.53	6.82	6.20
Maize yield	3.75	**8.97**	4.34	3.83	3.61	4.19	5.97	**16.76**
Rice yield	5.08	**13.65**	7.11	1.76	4.65	4.57	0.44	2.61
Wheat yield	4.03	**10.19**	**9.22**	2.49	**8.68**	**13.17**	**11.92**	**7.98**
Oil palm	0.85	6.27	-	0.72	-	2.56	-	1.13
Soy	1.81	2.56	1.77	0.78	7.53	**7.31**	6.69	**10.79**
LU history								
TFU	6.13	**9.24**	**12.40**	6.99	**9.30**	**16.72**	**10.97**	5.30
Island	0.64	-	0.02	-	0.01	0.36	-	-
Realm	**38.23**	-	-	-	-	-	-	-

***p<0.001

Trajectory analyses of past human land use as a tool to understand current distribution of terrestrial mammals

Polaina, E., González-Suárez, M. & Revilla, E. Trajectory analyses of past human land use as a tool to understand current distribution of terrestrial mammals (*In prep*).

Abstract

Apart from the known environmental factors influencing species richness distribution at the global scale, additional anthropogenic factors need to be considered in order to fully understand their current extents of occurrence. Namely, distribution of threatened species should be particularly influenced by human activities, since species are known to be in decline under their pressure. The role of current human activities in modelling species distribution has been often confirmed, but there is still a facet of land use that has not yet been sufficiently explored: land-use history. In the present work we investigate how recently published models of past land use from c.B.C.6000 to c.A.D.2000 can improve our understanding of current distribution of total and threatened terrestrial mammal species. We first identify three general human land-use trajectories representing *low*-, *recently*- and *steadily-used* areas. Additionally, we explore how indicators of total land-use area at different time spans, rates of change, duration of land use, and remarkable land-use events associate to distribution of total and threatened mammal richness. The three types of trajectory-cluster do not differ in terms of total or threatened mammalian richness; however, differences are identified regarding the weight of the contribution of past land-use metrics to explain distribution patterns of both groups of species. In general, past land-use area and rates of change are more relevant, with different time periods being determinant within each particular trajectory-cluster. On the other hand, distribution of threatened mammals is more influenced by past land-use indicators than total mammalian richness. Our results demonstrate the value of considering the past to understand the present which can improve our ability to formulate hypothesis about the fate species face, based on the trajectory they have already undergone.

Resumen

Aparte de los conocidos factores ambientales que influyen en la distribución de la riqueza de especies a escala global, hay factores antrópicos adicionales que deben ser estudiados para entender por completo estos patrones. En concreto, la distribución de especies amenazadas debería estar particularmente influenciada por las actividades humanas, ya que muchas especies están en declive por las presiones de éstas ejercen. El papel de las actividades humanas actuales en el modelado de la distribución de especies se ha confirmado en múltiples estudios, pero existe una faceta del uso del suelo que aún no se ha explorado lo suficiente: la historia de uso del suelo. En el presente trabajo investigamos cómo modelos recientemente publicados de uso del suelo pasado pueden mejorar nuestra comprensión sobre la distribución de mamíferos actual (total y amenazada). Primero identificamos tres trayectorias generales de uso del suelo humano que representan áreas *poco, recientemente y continuadamente usadas*. Además, exploramos cómo indicadores del área total usada en los distintos periodos, tasas de cambio, duración de uso, y eventos destacables de uso del suelo se asocian con la distribución de mamíferos actual (total y amenazados). Los tres grupos de trayectorias no presentan diferencias en términos de riqueza de mamíferos (total y amenazada); sin embargo, sí que identificamos diferencias respecto al peso de la contribución de los métricos de uso del suelo pasado para explicar los patrones de distribución de ambos grupos de especies. En general, el área usada pasada y las tasas de cambio son más relevantes. En cada uno de los grupos de trayectoria, el periodo temporal más determinante es variable. Por otro lado, la distribución de mamíferos amenazados se ve más afectada por el uso del suelo pasado que la distribución de mamíferos totales. Nuestros resultados demuestran que considerar el pasado para entender el presente puede mejorar nuestra habilidad para formular hipótesis sobre el destino al que se enfrentan las especies, basándonos en la trayectoria transcurrida.

Introduction

Threatened species are unevenly distributed across the world, with remarkable differences among taxonomic groups (Grenyer et al. 2006). If extinctions occur by chance, we would expect more threatened species in areas with higher species richness which is, in turn, largely determined by gradients in climatic conditions affecting the availability of energy and water (Hawkins et al. 2003; Terribile et al. 2009). However, the relationship between overall species richness and the number of threatened species remains unclear, with numerous studies revealing spatial incongruence (Orme et al. 2005; Ceballos & Ehrlich 2006).

Clearly extinctions do not occur by chance but are instead shaped by human activities, such as direct persecution or landscape modifications (Russell et al. 2013). Increased extinction risk may be first manifested as a higher number of threatened species, and ultimately can affect overall local or regional species richness. Therefore, both total richness and the number (or proportion) of threatened species might be related to the number and/or intensity of threats within a given area. Some previous studies have related factors such as accessibility, land cover or human land use to the distribution of vertebrates richness across biogeographic-realm and country-wide scales (Martins et al. 2014; Torres-Romero & Olalla-Tárraga 2014; Mouchet et al. 2015). Other studies have shown how the number of threatened species is associated to direct factors, e.g. human land use (Lenzen et al. 2009; Brum et al. 2013), and indirect proxies, e.g. human population or gross national product (Chapter 2; McKinney 2001; Naidoo & Adamowicz 2011; Polaina et al. 2015) at different biogeographic and political study units. Within the framework of spatial conservation planning, some authors have considered higher numbers of threatened species as an attribute to be prioritized (Bonn et al. 2002; Grenyer et al. 2006) indirectly assuming that good quality habitat is still present in those areas. However, recent studies on terrestrial mammals show that this relationship is actually more complex and non-linear, implying that in some regions more threatened species are found in areas where threats are abundant, whereas in other cases species persist in well-preserved *refuge* areas (Chapter 3). All in all, it seems clear that the relationship between threats and threatened species is not

simple at coarse spatial scales (well-beyond the population level), and that additional factors must be driving this relationship at a global scale. Additionally, it remains unclear whether threatening activities are directly related to distribution of total richness.

One of the factors that may help explain current biodiversity patterns is past human pressure (Faurby & Svenning 2015b). Since the beginning of sedentary human societies and the advent of agriculture, around B.C.8000-6000, the amount of land under human dominance has grown at an increasingly fast pace (Ellis 2011). Some events marked particularly notable transitions, such as the European invasions of many areas in the XV century, the XIX century industrial revolution with its productive, technological and demographic shifts and, more recently, the green revolution that triggered the so-called great acceleration (c.A.D.1950, Steffen et al. 2015). Throughout all this time, the evidence of the impact of humans on the conservation of mammals has becoming apparent: the extinctions of megafauna in the Late Pleistocene-early Holocene (~B.C.8000; Sandom et al. 2014); the declining trend of populations of many species in Europe coinciding with the decline of forested area (c.A.D.1000, Kaplan et al. 2009; Crees et al. 2016); and the range contractions of many species after European settlement in North America (Laliberte & Ripple 2004). Beyond the impact of the current human footprint, past human-induced events are potential drivers of the present biodiversity patterns at broad scales (Loehle & Eschenbach 2012; Faurby & Svenning 2015b).

All in all, the literature has offered evidence that current biodiversity patterns, including species richness and extinction risk distribution, are influenced by current anthropogenic activities. The effect of past human activities remains less clear, partly because broad-scale data on past human activities, such as land use, have only recently become available for temporal series of more than a century (Goldewijk et al. 2010; Kaplan et al. 2011). A few studies have explored the importance of past land use with mixed results (Chapter 3; Dullinger et al. 2013), which may be due to true variation in the role of past land use but also due to the type of metrics employed.

The present study aims to provide a description of global patterns in past land use using different metrics and proposing approaches to define trajectories, with the

final goal of exploring how these metrics may contribute to our understanding of biodiversity patterns. We use terrestrial mammals as a model group of study because their present conservation status and past dynamics of decline are generally well understood (Turvey & Fritz 2011; Prescott et al. 2012; IUCN 2014). First, we propose and apply a new approach to group human land-use trajectories based on a common history of land-use extent expansion and/or reduction. We define trajectories according to observed changes in the portion of land classified as used by humans at different time spans ranging from c. B.C.6000 to c. A.D.2000. Second, we investigate differences in total mammalian richness and number of threatened species among these defined trajectory-clusters. Finally, we explore differences in distribution of total and threatened mammalian richness within trajectory-clusters considering current human land use and different past land-use indicators.

The analyzed indicators are based on four general descriptors of past land use that we hypothesize could affect current observed distribution of mammals richness: 1) total land-use area: if there is a time lag between human pressures and species responses, past human land use extent may explain species richness distribution better than present land use; 2) rate of land-use change: if rapid changes limit the ability of species to respond via adaptation, areas that had been modified at a faster pace may have fewer and more threatened species today; 3) duration of human settlement: if extended modification and pervasive human presence increase risk of extinction, areas modified for longer periods may be more likely to have impoverished fauna and more threatened species; and 4) remarkable land-use events: if intense past human impacts, even if later reversed, have lasting and irreversible effects, areas in which extensive land use occurred in the past may have fewer total and more threatened species.

Methods

Data sources

Data of total proportion of land use per grid cell (see below) at different time spans was obtained from Ellis et al. (2013; available at <http://ecotope.org/products/datasets/used_planet/>). We chose the KK10 model

(Kaplan et al. 2011) which assumes that humans use land more intensively when population density is high and land scarce (Boserup 1965). The other available historical land-use global dataset (Historical Data base of the Global Environment, HYDE; Goldewijk et al. 2010) provides predictions based only on nearly linear relationships between human population density and land use and thus, we considered it to be less comprehensive. The selected dataset describes ten time breaks: B.C.6000, B.C.3000, B.C.1000, A.D.0, A.D.1000, A.D.1500, A.D.1750, A.D.1900, A.D.1950 and A.D. 2000. The last period will be referred as 'present' for the purpose of this work. The original resolution of the dataset is 5 arc minute, which was recalculated for a grid of 1x1º (geographic projection) projected into Berhmann cylindrical equal area as the mean value for each grid cell and for each time period. Each grid cell presents a surface of approximately 110 x 110 km (≈ 12,100 km^2). Cells with an emerged area smaller than 10,000 km^2 were excluded to approximate equal-size samples. This resolution was selected given that terrestrial mammals' geographic ranges would not allow a finer resolution without overestimating species richness (Hurlbert & Jetz 2007). Data are expressed as the proportion of land intended for human use at each time break.

Terrestrial mammal species' distributions (extent of occurrence) were obtained from the International Union for Conservation of Nature (IUCN 2014), selecting only native, extant and probably extant areas. Distribution data were intersected with the grid, and species were considered as present in a particular grid cell when any overlap existed. Threatened mammals are those categorized as vulnerable (VU), endangered (EN) or critically endangered (CR) by the IUCN (IUCN 2014). Total richness was the sum of all terrestrial mammal species occurring in a grid cell.

Statistical analyses

To describe trajectory trends in longitudinal data of global land use we employed a clustering method that incorporates a *k*-means algorithm (Celeux & Govaert 1992) implemented in the *kml* package ('kml' function; Genolini et al. 2015) in R v.3.2.3 (R Core Team 2015). This method allowed us to group grid cells with similar trajectories

along the considered temporal range (B.C.6000 - A.D. 2000). The optimal number of clusters was defined using five non-parametric quality indices that allow for the selection of the best number according to different criteria: three variants of the Calinski & Harabanz criterion, the Ray-Turi criterion and the Davies-Bouldin criterion (Calinski & Harabasz 1972; Davies & Bouldin 1979; Ray & Turi 1999; Kryszczuk & Hurley 2010). All of them try to minimize the within-cluster compactness whereas maximizing the among-cluster spacing, and are standardized within the *kml* package to allow comparisons (Genolini et al. 2015). This method allowed to easily classifying areas that had followed similar land-use transformations across time.

Once *trajectory-clusters* were delimited, we fitted global models, including *trajectory-cluster* as an additional categorical predictor, to search for differences among clusters. We then fitted separated models by cluster, to further investigate differences within *trajectory-clusters*. Differences were measured in terms of total mammalian richness and numbers of threatened mammals. To do so, we fitted two blocks of model: 'null' models, exploring the effect of latitude, present land use and total mammalian richness (the latter only considered when modelling number of threatened mammals); and 'past-land-use' models, which expanded the null models to explore the relevance of additional indicators of past land use (Fig. 4.1).

Latitude was included to account for the known latitudinal gradient in species diversity distribution (Rohde & Dec 1992; Hillebrand 2004) and was measured in degrees. Total mammalian richness controlled for the fact that the number of threatened species is highly dependent on the total number of species within an area. Portion of present human land use (per grid cell) was used as a reference, given its known importance as an anthropogenic driver of habitat loss and deterioration (Foley et al. 2005). We defined present use as the value of human land use at c.A.D.2000 in the analyzed database (Ellis et al. 2013).

Indicators included in past-land-use model accounted for the four hypotheses presented in the introduction: 1) past land-use extent at the different time breaks, 2) rates of change in human land use for different prehistoric and historic periods, 3) duration of human settlement, and 4) remarkable land-use change (Table 4.S1). Past land-use extent was obtained as described above. Land-use rates of change were

calculated as the difference in the portion of a grid cell defined as used in a given time period standardized per 1000 elapsed years (Table 4.S1). Time periods were defined as: prehistoric (c.B.C.6000-c.A.D.0), pre-industrialization (c.A.D.0-1750), industrialization (c.A.D.1750-1950) and post-industrialization (c.A.D.1950-2000). Duration of human settlement was calculated as the number of years since time of first significant use (TFU), where TFU was defined as the time more than 20% grid cell was used following Ellis et al. (2013) and calculated as the number of years that this value was maintained or exceeded. The maximum land use value for the whole time series (LU_{max}) was used to categorize remarkable land-use change. We considered relative remarkable values because land use patterns are globally heterogeneous (the maximum in one region could be similar the minimum in another) and using a unique level of use would not represent this diversity.

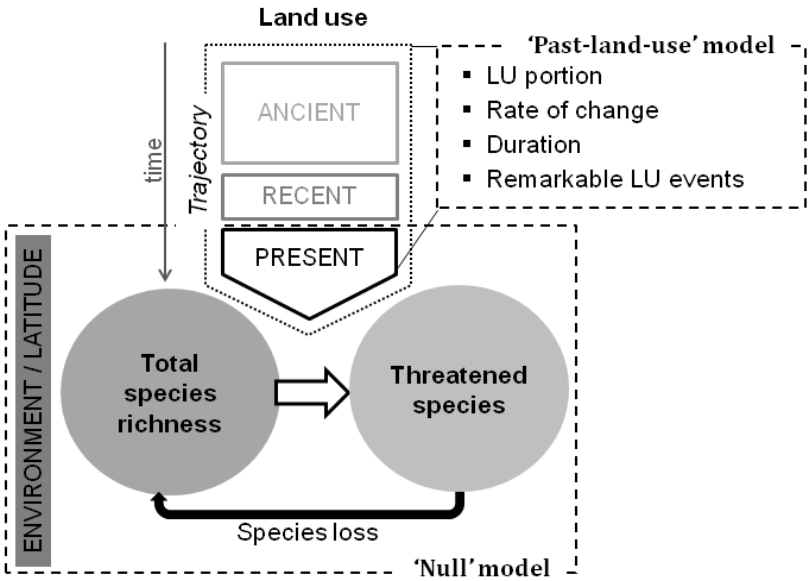


Figure 4.1. Conceptual framework of the relationships explored in the present work. 'Null' model includes latitude, present land use and total mammalian richness (when not included as the response variable). 'Past-land-use' model includes those predictors plus 9 variables of portion of human land use, corresponding to 9 time periods; 4 rates of land-use change, corresponding to 4 temporal periods; 1 measure of duration (since time of first significant use); and 1 measure of remarkable land use (maximum). *LU*, land use.

Both blocks of models were fitted first for all grid cells and then separately by cluster, using boosted regression trees (BRT) where the response variables were either total mammalian richness or number of threatened mammals. BRT were used because these methods are better suited to evaluate correlated predictors and allow to explore non-linear relationships (Elith et al. 2008a). To fit the models we used the function 'gbm.step', which calculates the optimal number of trees using 10-fold cross validation, and it is included in the *dismo* package (Hijmans et al. 2013) in R. A Poisson error structure for the response variable was assumed, a bagging fraction of 0.5, a tree complexity of 5 and a learning rate of 0.005 (Appendix 4.S3). These parameters were fixed according to the guidelines in Elith et al. (2008) to achieve a minimum of 1000 trees. To account for spatial autocorrelation, all models included a residuals-based autocovariate (RAC) that specifies the relationship between the value of the residuals at each location and those at neighboring locations (the 8 immediate grid cells surrounding each cell as neighbors, approximately within a 165 km distance in our case). Deriving the autocovariate from the residuals allows to include only the remaining deviance unexplained by the explanatory variables, thus the actual influence of the predictors is better captured (Crase et al. 2012). Cells containing a proportion of threatened mammals greater than 0.999 were excluded from the analyses (N=12). A predictor was considered to be relevant when its relative importance was greater than expected by chance (100% divided by the number of variables included in each model; e.g. Müller et al. 2013).

Results

All quality criteria supported the differentiation of three trajectory-clusters describing global temporal patterns in past land use from c.B.C.6000 to c.A.D.2000 (Fig. 4.S1). These three trajectory-clusters correspond to three broad global patterns of land-use progression (Fig. 4.2A): *low-used areas* (51.9% of grid cells) where land-use values were low showing only small increases in use over time and apparent moderate declines at present; *recently-used areas* (32.3% of grid cells), where the rate of land encroachment was moderate until relatively recent times (~A.D.1750) when a strong increase in land

use was observed; and *steadily-used areas* (15.8% of grid cells), where initial land use was higher than in the rest of trajectories and increased at a relatively constant rate with a soft steepening around B.C.1000 and a recent decline. Most grid cells within *low-* and *recently-used* areas were first significantly used by A.D.1900 (FU; >20% grid cell), whereas in *steadily-used* areas, this had already happened by B.C.3000 (Table 4.S1). Once FU is achieved, this level was normally maintained to the present, except for some *low-used* areas, where a reversion often took place (Table 4.S1). Maximum land use (LU_{max}) was mainly achieved in present times (c.A.D.2000) in most parts of the world, excluding *steadily-used* areas, where most of cells reached the LU_{max} on A.D.1750 (Table 4.S1). It is worth mentioning that the later the maximum was achieved, the higher its value within each trajectory-cluster (Fig. 4.S8). *Low-used areas* are mainly located in regions of low primary productivity, such as deserts and boreal forests; but also in productive biomes that may have remained largely unused due to difficulties for humans to access them, like the tropical forests of Borneo and the Amazon (Fig. 4.2B). *Steadily-used areas* include the main cradles of ancient human settlements, including parts of the Middle East, Europe, India, eastern China, the Sahel and Central America. *Recently-used areas* largely correspond to territories of relatively modern human colonization and expansion, such as North America, Australia or southern and East Africa (Fig. 4.2B). While quality criteria supported three clusters, there were additional configurations that had partial support. These are described in Appendix 4.S1. Essentially, further division of *recently* and *steadily-used areas* occurs when more clusters are defined, whereas *low-used areas* remain as a single group independently of the number of chosen clusters (Fig. 4.S2).

Global 'null' models showed no relevance of the *trajectory-cluster* to explain total mammalian richness or numbers of threatened mammals (Table 4.1). Total mammalian richness is, as expected, predominantly influenced by latitude; and numbers of threatened species are greatly driven by total richness. The same general trends hold on separated trajectory-cluster 'null' models, with some differences among clusters. Latitude presents a clear influence on total mammalian richness on all trajectory-clusters, being greater in *low-used* areas (65.95% variable importance) than in *steadily-used* (55.95%) and *recently-used* areas (43.70%; Table 4.1). Total mammalian

richness, the most important predictor of numbers of threatened mammals, is more relevant in *low-used* areas (53.53%), than in *recently-* (41.32%) or *steadily-used* areas (33.06% Table 4.1). The RAC term presents high relative importance in all models, with a minimum contribution of 28.38% within *low-used* areas. The explained deviance for models with threatened mammals as a response is higher in *low-used* areas, followed by *steadily-used* areas and *recently-used* areas. To explain total mammalian richness, the model of *low-used* areas is again better, followed by the *recently-used*-areas model and the *steadily-used*-areas model (Table 4.1).

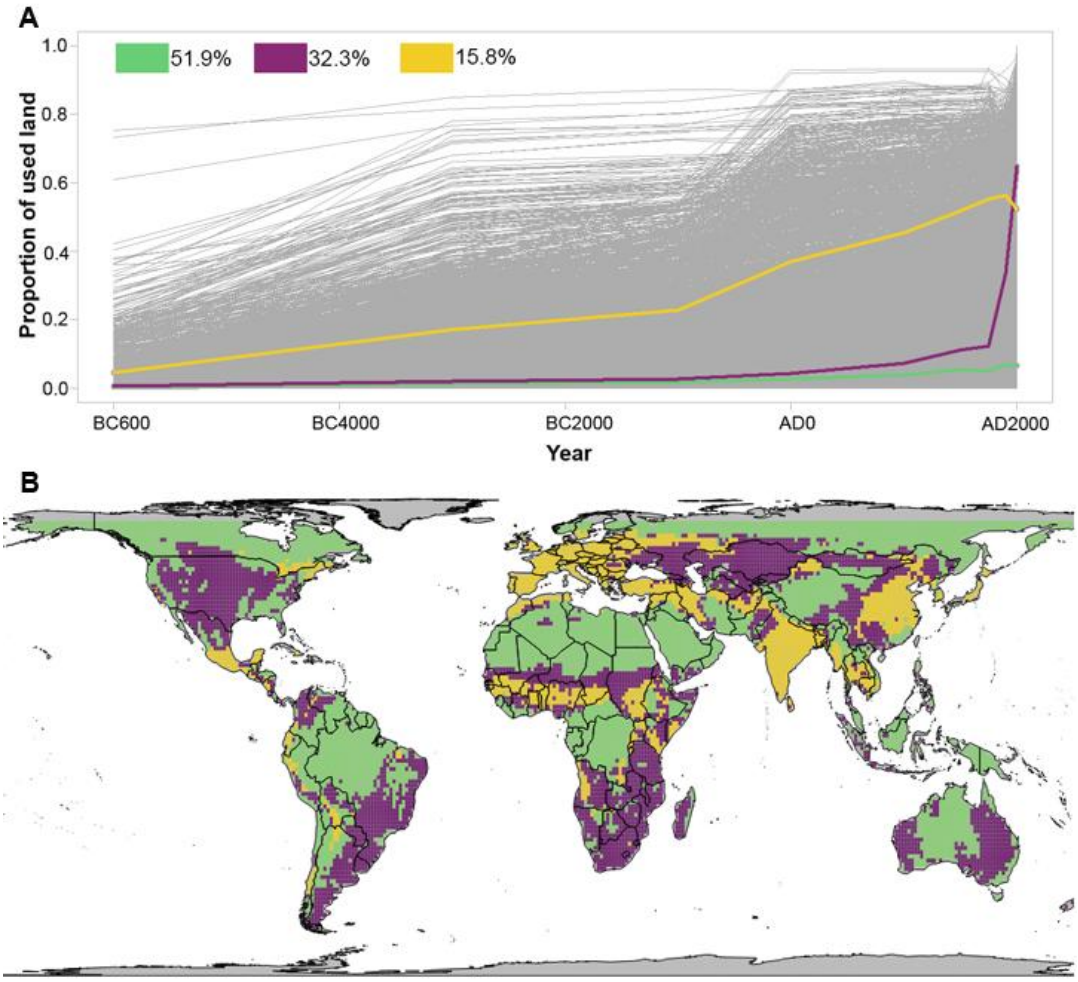


Figure 4.2. Overall trajectories (A) and spatial location (B) of land-use trajectories from B.C.6000 to A.D.2000. Three was the optimal number of clusters according to the different quality criteria implemented in *kml* package (Genolini et al. 2015). In panel A, X axis represent the approximate year for which land use estimations are available in the KK10-model database, and Y axis the

proportion of land use (% grid cell); legend shows the proportion of grid cells (one for each grey line) assigned to each trajectory-cluster. The green line represents the average trajectory for *low-used areas*, the purple line the average of the *recently-used areas,* and the yellow lines the average *steadily-used areas.* Panel B represented with Berhmann cylindrical equal area projection.

Table 4.1. 'Null' model. Results from the BRTs global and by trajectory-cluster (*low, recently* and *steadily used*) including latitude, total mammalian richness and present land use (c.A.D.2000) as predictors. Two response variables were explored, number of threatened mammals and total mammalian richness. *Variable importance* quantifies the effect of each variable on prediction. *Number of trees* is the optimal number over which final results are drawn. *Explained deviance* is the model explanatory power, respect to the null deviance is the initial value before any split is made (further details on BRT are described in Appendix 4.S3).

	Threatened				Total richness			
Variable importance	Global	Low	Recently	Steadily	Global	Low	Recently	Steadily
Latitude	12.89	12.80	16.66	18.35	45.23	65.95	43.70	55.95
Total richness	44.22	53.53	41.32	33.06	-	-	-	-
Present LU_{AD2000}	1.83	5.28	5.84	4.46	3.86	3.20	4.35	4.02
RAC[1]	40.56	28.39	36.18	44.12	50.04	30.85	51.95	40.03
Trajectory-cluster	0.49	-	-	-	0.86	-	-	-
No. trees	7800	7200	8250	6000	6000	3900	4400	4400
Explained deviance	91%	92%	84%	87%	96%	96%	92%	89%

[1]Residual autocovariate

Apart from the assessing predictor importance, we were interested in exploring their relationship with the two biodiversity metrics: threatened mammals and total mammalian richness; which can be visualized by plotting partial dependency plots (PDP) from BRTs which consider the effect of one variable holding the rest at their mean value. Variables from the 'null' model show interesting patterns. Mammalian richness is higher around the Equator (Fig. 4.3B), and in areas where present land use is relatively low within *steadily*- and *recently-used* areas, whereas in *low-used* areas, richness is higher in more used areas (although this level is well-below the values in the other clusters; Fig. 4.3D). Threatened mammals are generally more numerous in northern latitudes –especially in *steadily-used* areas (Fig. 4.3A). The association between present land use and threatened mammals varies across trajectory clusters but peaks generally occur in areas with 25-50% of current use defined as human (Fig.

4.3C). The relationship between total mammalian richness and numbers of threatened species is always positive, with slightly more predicted threatened mammals for the same richness within *steadily-used* areas (Fig. 3E).

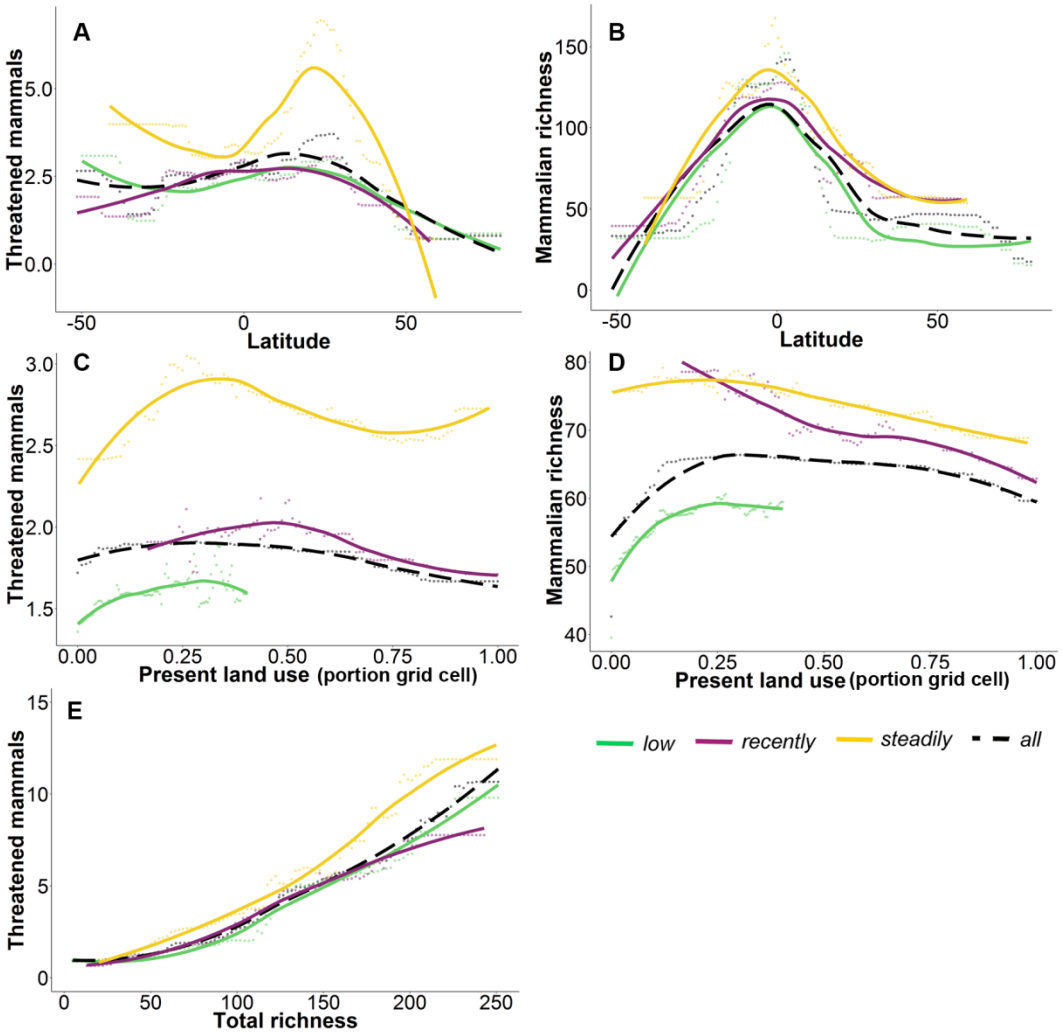


Figure 4.3. Partial dependency plots (PDP) of predictors from the 'null' model: latitude (A and B), present land use (C and D) and total mammalian richness (E). Left column corresponds to results from the BRT fitted for threatened species, and right column to BRT using total mammalian richness as a response. BRT models where separately fitted for all grid cells (black), low- (green), recently- (purple) and steadily- (yellow) used areas.

'Past-land-use' BRTs showed relative low relevance of tested metrics of past land use, both globally and by trajectory-cluster, in determining threatened and total mammalian richness distribution. Top predictors identified in the 'null' model

remained as most important (total mammalian richness to explain numbers of threatened mammals, and latitude to determine total mammals), and trajectory-cluster still did not show any relevance to explain mammals' diversity metrics (Figs. 4.4 & 4.5; Table 4.S2). However, there were some interesting patterns worth discussing. First, past land use variables explained previously unaccounted for variance, reflected by the RAC term, which was the only variable to change its importance noticeably for both response variables (total and threatened richness). Second, past land-use indicators were considerably more important than present land use (A.D.2000), which was also not identified as relevant in the 'null' models (Figs. 4.4 & 4.5; Tables 4.1 & 4.S2).

Overall, no single descriptor of land use was clearly the best. In explaining numbers of threatened mammals, rates of land use change were generally more relevant than past land-use extent, duration of significant land use, or remarkable land use (Fig. 4.4). Namely, pre-industrial rate of change (c.A.D.0-1750) was important within *low-* and *steadily-used* areas; and prehistoric land-use change (c.B.C.6000-A.D 0) and portion of human land use c.B.C.600 within *recently-used* areas. On the other hand, total mammalian richness was importantly driven by the proportion of land use on c.A.D.1500 within *low-* and *recently-used* areas, and additionally by pre-industrial rate of change within *low-used* areas (Fig. 4.5).

Discussion

Our results show that land use history across the world can be broadly summarized into three trajectory-clusters: *low-*, *recently-* and *steadily-used* areas. Although there are not net differences in total and threatened terrestrial mammals among clusters, as shown by global models; within clusters, there are disparities in the weight different predictors have in explaining both diversity metrics and also in the shape of the relationship between predictors and responses. Generally, *low-used* areas are more influenced by 'null' predictors (i.e. latitude for total richness and total richness for threatened species) than the rest of the trajectory-clusters, and *recently-* and *steadily-*

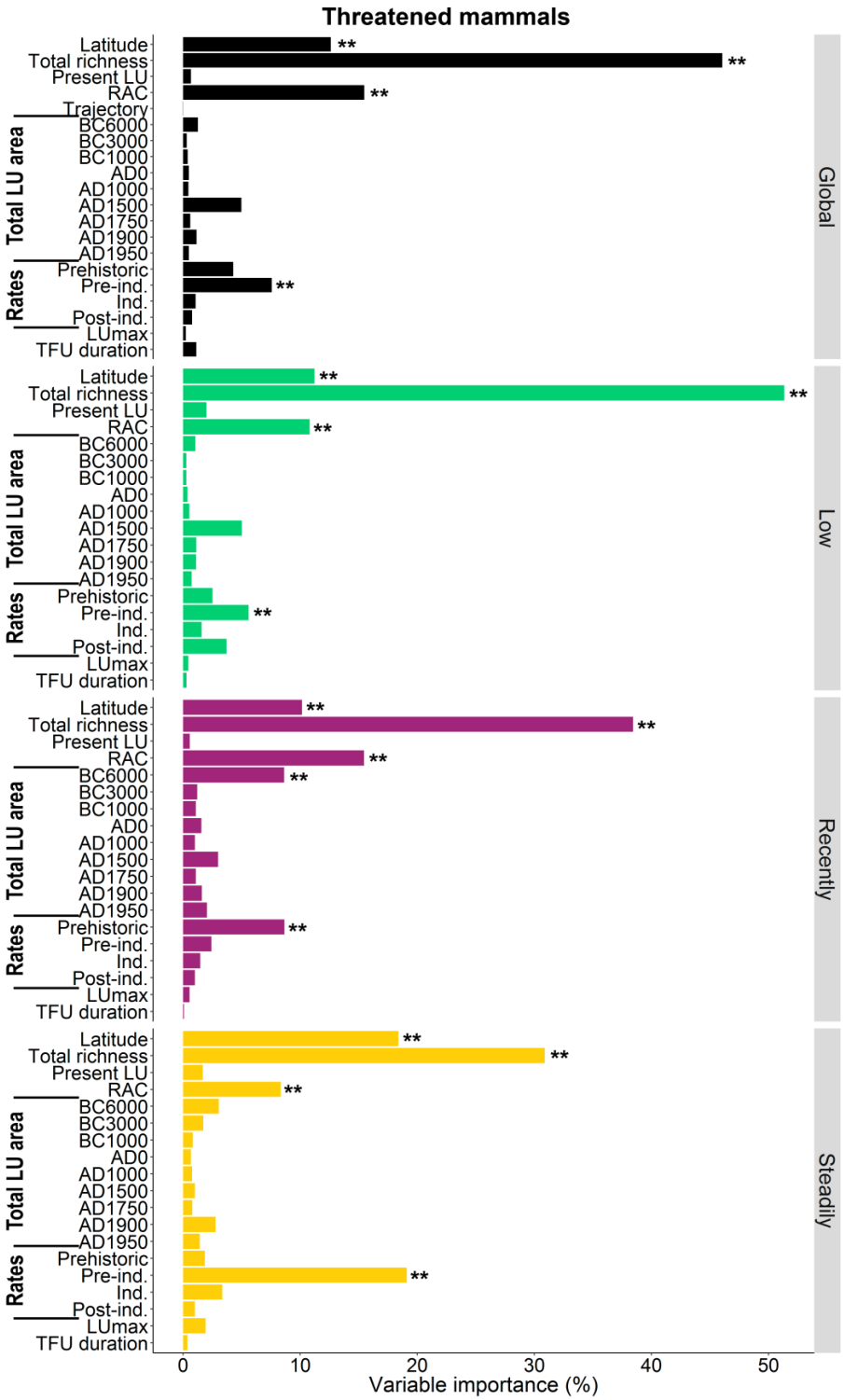


Figure 4.4. Relative variable importance for global and trajectory-cluster BRT, fitted for threatened mammals as the response variable. Black color displays results from the global BRT, green from the *low-used* areas, purple from *recently-used* areas, and yellow from *steadily-used* areas. Two asterisks mark relevant predictors (>100%/total number of variables).

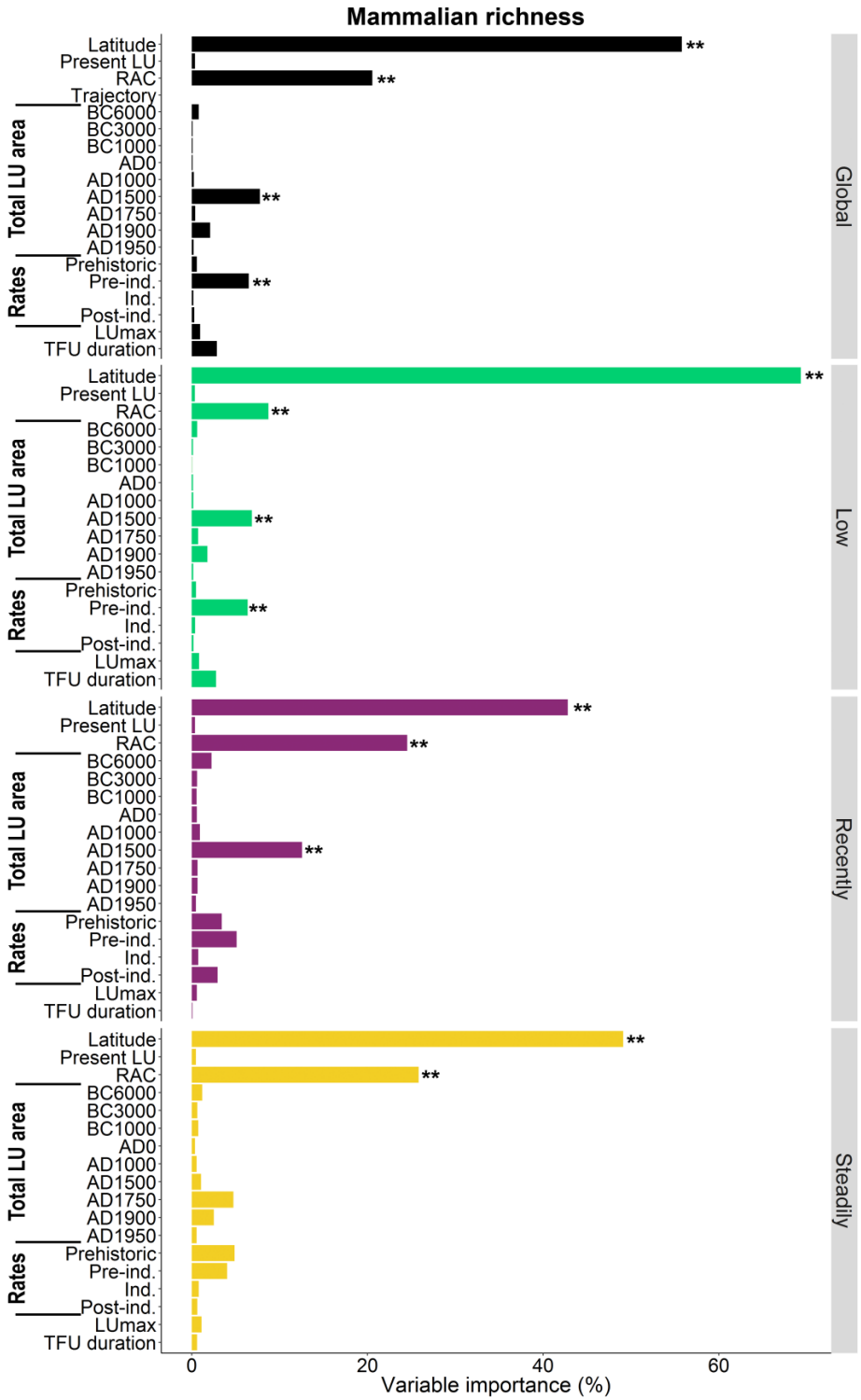


Figure 4.5. Relative variable importance for global and trajectory-cluster BRT, fitted for total mammals as the response. Black color displays results from the global BRT, green from the *low-used* areas, purple from *recently-used* areas, and yellow from *steadily-used* areas. Two asterisks mark relevant predictors (>100%/total number of variables).

used areas show a higher importance of past land-use changes to explain numbers of threatened mammals. Past land-use indicators are overall more important in explaining total and threatened mammalian richness than present land use. Besides, the inclusion of past land-use metrics reduces the uncertainty associated to spatial autocorrelation (generated by different environmental and ecological factors, that may be very complex to model), which suggests that part of the otherwise unexplained spatial variation may be consequence of a shared land use history. Indicators of past land use are, in turn, more relevant to explain numbers of threatened mammals than to explain total mammalian richness.

Low-used areas

According to our results, more than 50% of land areas (excluding Antarctica and most of Greenland) have followed a *low-used* trajectory. These regions broadly coincide with last-of-the-wild areas, traditionally seen as opportunities to preserve biodiversity given the relatively low human influence to which they are exposed (Sanderson et al. 2002). Lack of historical human pressure may be explained by two different reasons: little primary productivity associated to biomes of the northern hemisphere, such as the Taiga and the Tundra, or different deserts worldwide (Fig. 4.2); and relative remoteness, such as tropical forests, e.g. Amazon. Despite the relatively low current human influence, these areas are exposed to two clearly different scenarios of global change: the first are relatively safe in terms of competition for land by humans, although they may severely suffer from global warming (Imhoff et al. 2004; Anderegg & Diffenbaugh 2015). On the other hand, tropical regions such as the Amazon, South-Central Africa or the islands of Borneo and Papua-New Guinea are increasingly losing natural forests (Bird et al. 2012), something that can already be observed looking at land use c.A.D.2000, where the portion of human land use is much higher in tropical regions than in northern latitudes within *low-used* areas (Fig. 4.S4). As a result, these areas, whose mammalian diversity distribution appears mainly determined by natural factors as shown by our results, may be soon driven by additional anthropogenic factors that are already exerting pressure on those systems.

Low-used areas present a soft latitudinal gradient for threatened mammals, and a more 'traditional' one for total mammalian richness (Figs. 4.3A and B). On the other hand, areas with higher human land use have higher richness, but also higher numbers of threatened species (Figs. 4.3C and D), which may suggest that local extinctions have not yet taken place and that there is an extinction debt in more used areas within this trajectory-cluster, such as in parts of the Amazon or the Congo Basin (Kuussaari et al. 2009). However, it is important to notice the low relevance of this variable in explaining both total and threatened mammalian richness distributions. Although past land-use indicators are not very relevant within this trajectory-cluster compared to the rest, it is worthy to mention the key temporal segment starting from c.A.D.0 to c.A.D.1750, both in terms of land-use change during the preindustrial period and the actual land use value at c.A.D.1500. Apparently, changes in the Congo Basin, the Nepal-South-East-China area and external parts of the Amazon were relatively high during that period (Fig. 4.S5), which may have left a mark on mammalian species composition.

Recently-used areas

Around 32% of land follows a *recently-used* trajectory; these are areas humanized after the great colonization events of the 15th century onwards. Today, they do not present particularly high species richness or accumulations of threatened mammals (Fig. 4.S3), thus they are not generally considered a global priority, except for a few particular cases (Brooks et al. 2006). The humanization of these areas after the colonial era was huge. Many of these regions are highly developed countries, such as the United States or Australia, or at least moderately, like South-Africa (Fig. 4.2).

Again, the species richness latitudinal gradient holds for total mammals but varies for only threatened mammals. Higher current human land use associated with lower total mammalian richness, and the number of threatened mammals follows an inverted-U shape, with a potential peak around 0.5 portion of use (Figs. 4.3 C & D). This suggest that local extinctions may have occurred, with most sensitive species (threatened) being still present at intermediate stages of human land use but disappeared at extremely high values. Past land-use models reveal the apparent

importance of the prehistoric period (both in terms of land use and land-use change) in explaining numbers of threatened mammals and land use c.A.D.1500 in explaining total mammalian richness. This seems counterintuitive for areas that have predominantly been used after cA.D.1750; however, some studies have found that terrestrial mammals losses in places like Australia or New Guinea predominantly occurred during the prehistory (Faurby & Svenning 2015b).

Steadily -used areas

Less than 16% of global land belongs to this trajectory-cluster, which is characterized by a relatively high and long-lasting human encroachment of land. Steep changes have not generally taken place, although the average level of human appropriation of land within these areas by A.D.0 has not even been reached by *low-used* areas at present (Table 4.S1). As in previous cases, there is spatial heterogeneity within this trajectory-cluster which includes tropical and temperate regions.

These areas show a common latitudinal gradient regarding distribution of total mammals, however higher numbers of threatened mammals tend to concentrate in northern latitudes, e.g. Europe. This does not mean that Europe has more threatened mammals than India or Asia in *steadily-used* areas, but that once total mammalian richness, present land use and latitude are taken into account, these areas present relatively more threatened mammals. As for present land use, —despite its low contribution to explain mammalian diversity— threatened species tend to be more numerous either at relatively low values (~0.25 portion of human land use) or at very high values (~1.0 portion of human land use). Total mammalian richness is higher when human land use is relatively low. Thus, relatively low used areas are still rich in mammals and therefore more of them are threatened; whereas in areas widely modified, richness is already low because many species have been lost and the remaining sensitive species coexist with threatening human activities (Chapter 3). Only one past land-use indicator is relevant in determining threatened mammals distribution, i.e. the preindustrial rate of land-use change. Total mammalian richness is nearly independent of present and past human land use, with a high relevance of environmental variables not included in the analyses (RAC term; Fig. 4.5).

In conclusion, past land-use metrics can partly improve our understanding of patterns of mammalian distributions, even though their importance is relatively minor compared to traditional correlates of species distribution, such as latitude or total richness in the case of threatened species. Nevertheless, we show that many of these metrics are more relevant in explaining total and threatened mammalian richness distributions than present land use. This has profound implications for future studies given the widespread practice of including present land use as a predictor of numbers of threatened species (Lenzen et al. 2009; Koh & Ghazoul 2010; Brum et al. 2013). Some previous studies, carried out at the continental scale have shown the greater relevance of past land-use metrics compared to present ones, however these studies were conducted using countries as units of study, which can be heterogeneous, vary in size and fail to capture past pattern of human pressure because current political boundaries may not reflect historical processes (Dullinger et al. 2013). From the past land-use indicators tested in the present work, past land-use extent and rates of land-use change more frequently appear as relevant to explain distribution of total and threatened terrestrial mammals. While this cannot directly been transferred into other spatial scales, it provides insights into the types of metrics that can be informative in explaining species distributions. In particular, the rate of change during the period c.A.D.0-1750 repeatedly appears as relevant highlighting the relevance of this period, at least within *low-* and *steadily-used* areas. The understanding of the land-use processes previous to industrialization, which may not be as catastrophic as the ones occurring afterward, may give us clues to explain current biodiversity patterns (Redman 1999). Duration of human land-use settlement does not seem to have an impact on global mammalian distribution patterns, probably because very ancient impacts on the environment were orders of magnitude lower than the ones experienced today or because the signal from those long-past events has been erased by more recent changes. The same explanation holds for the lack or relevance of the maximum land-use value as a predictor of threatened/total mammalian distribution. Importantly, in most of cases the maximum use occurred very recently, thus any effects on species distribution may not yet be observed (Brooks et al. 1999). Thus, it may be the case that present abrupt changes in relative untouched areas are much

more harmful than those that took place in a distant past and has prevailed until now (whose species may be tolerant to humans, having already passed an extinction filter; Balmford 1996; Turvey et al. 2011); however consequences are not yet apparent.

To our knowledge the presented trajectory-clusters' delineation has never been applied in biogeographic or ecological studies. We show this can be a powerful method to synthesize complex information. Its application at finer scales may allow disentangling differences in diversity patterns at local or regional scales, at which specific prehistoric and historic events can be matched to those patterns. Our results offer an interesting picture at a global scale, which could be further tested by using alternative data sources of past land-use (Goldewijk et al. 2010). Transformation of the biosphere by human is a very complex process, thus not direct causal effects may be inferred (Ellis 2011); still, general dominance of certain indicators allows to focus our research in particular temporal gaps within different regions of the world.

Acknowledgements

We thank the IUCN Red List team for making and maintaining its database freely available online. We also acknowledge the Laboratory for Anthropogenic Landscape Ecology, directed by Dr. Erle C. Ellis, for publicly sharing anthropogenic land cover change datasets. This work was funded by the program '*Junta para la Ampliación de Estudios*' (JAEPre022. BOE-A-2011-10745, co-funded by the European Social Fund), the European Community's Seventh Framework Programme (FP7/ grant n° 235897 and EU BON project nº 308454), and the Spanish Ministry of Science and Innovation co-funded by FEDER (CGL2009-07301/BOS, CGL2012-35931/BOS and JCI-2011-09158).

Supporting Information

Appendix 4.S1. Additional results of the trajectory-cluster analyses

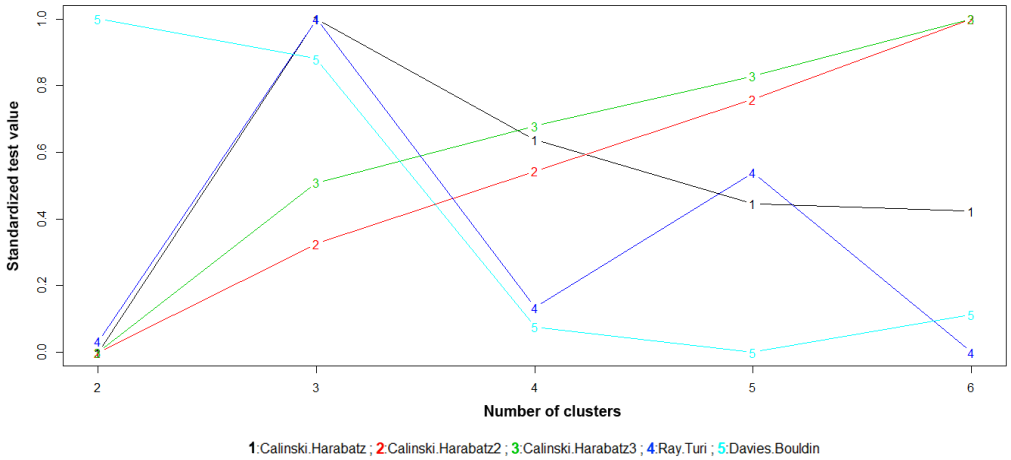


Figure 4.S1. Optimal number of trajectory clusters according to different criteria. X-axis represent the number of clusters, Y-axis shows the standardized [0-1] test values (the higher, the better). Different numbers and colors represent different quality tests, 1(black): Calinski-Harabatz (Calinski & Harabasz 1972); 2 (red): Calinski-Harabatz2, Kryszczuk variant (Kryszczuk & Hurley 2010); 3 (green): Calinski-Harabatz3, Genolini variant; 4 (blue): Ray-Turi (Ray & Turi 1999); 5 (cyan): Davies-Bouldin (Davies & Bouldin 1979).

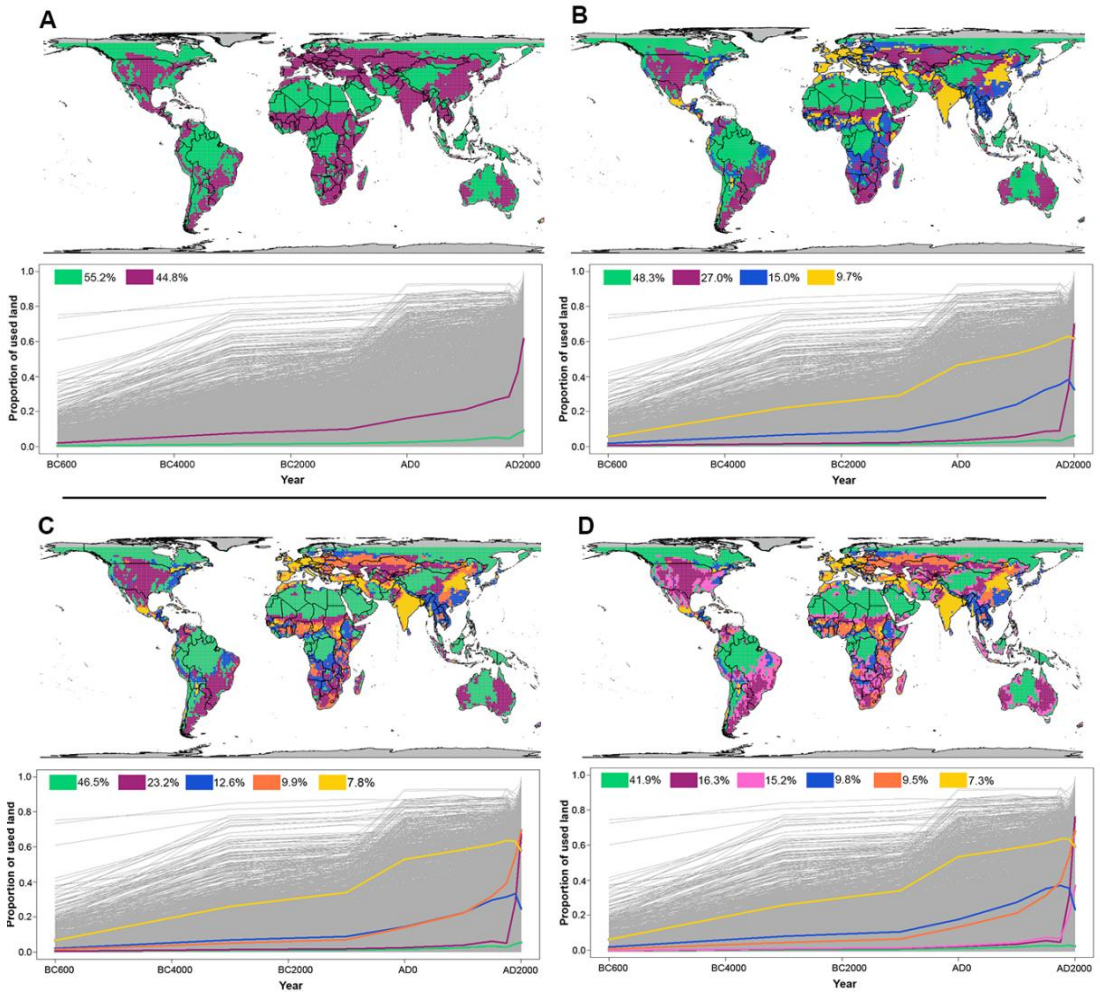


Figure 4.S2. Spatial location and overall trajectories of land use trajectories from B.C.6000 to A.D.2000, considering two (A), four (B), five (C) and six (D) cluster divisions. In all plots, X axis represent the approximate year for which land use estimations are available in the KK10-model database, and Y axis the proportion of land use (% grid cell). Legend shows the proportion of grid cells assigned to each trajectory-cluster. Projection: Berhmann cylindrical equal area.

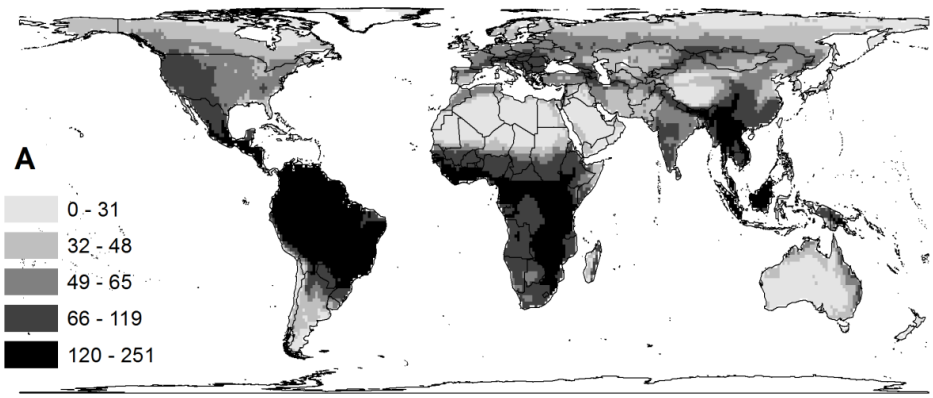
Appendix 4.S2. Data description: global and by trajectory-cluster

Table 4.S1. Description of indicators of land use, calculated for a grid of ~110x100km , based on the KK10 model (Kaplan et al. 2011; spatial data avilable at <http://ecotope.org/anthromes/data/)>). *Land use* refers to the mean proportion of grid cell classified as used at each time break (original temporal resolution); *land use change* was calculated as the difference of proportion of used grid cell between temporal milestones, standardized per 1000-years time; *remarkable land use* considered are: first significant use and maximum land use. *Time* (when the value took place), *duration* (number of years and percentage of time until present that this value was maintained ±0.2 portion of grid cell), and *peak value* (actual value of the portion of grid cell that is the first use of the maximum).

	Global	Low used (N=5119)	Recently used (N=3189)	Steadily used (N=1559)
Land use [median, min-max (portion of grid cell)]				
BC6000	0.004 (0-0.754)	0.001 (0-0.181)	0.004 (0-0.169)	0.024 (0.002-0.754)
BC3000	0.008 (0-0.848)	0.004 (0-0.332)	0.009 (0-0.230)	0.138 (0.003-0.848)
BC1000	0.012 (0-0.871)	0.005 (0-0337)	0.012 (0-0.278)	0.204 (0.003-0.871)
AD0	0.019 (0-0.928)	0.009 (0-0.380)	0.021 (0-0.323)	0.347 (0.016-0.928)
AD1000	0.034 (0-0.930)	0.013 (0-0.392)	0.046 (0-0.380)	0.435 (0.102-0.930)
AD1500	0.055 (0-0.931)	0.018 (0-0.442)	0.082 (0-0.609)	0.494 (0.166-0.931)
AD1750	0.034 (0-0.936)	0.011 (0-0.520)	0.057 (0-0.559)	0.547 (0.108-0.936)
AD1900	0.197 (0-0.928)	0.030 (0-0.491)	0.314 (0-0.783)	0.560 (0.203-0.928)
AD1950	0.247 (0-0.946)	0.023 (0-0.332)	0.490 (0.271-0.853)	0.556 (0.144-0.946)
AD2000	0.251 (0-1)	0.005 (0-0.404)	0.652 (0.166-1)	0.538 (0.003-0.979)
Land-use change [median, min-max (portion of grid cell·1000 yr)]				
Total[1]	0.238 (-0.379-0.999)	0.002 (-0.166-0.402)	0.646 (0.16-0.999)	0.496 (-0.379-0.955)
Prehistoric[2]	0.014 (0-0.857)	0.006 (0-0.373)	0.016 (0-0.311)	0.298 (0.014-0.857)
Historic[3]	0.117 (-0.777-0.982)	-0.001 (-0.37-0.4)	0.612 (-0.013-0.982)	0.147 (-0.777-0.845)
Pre-industrialization[4]	0.005 (-0.280-0.832)	0.001 (-0.164-0.503)	0.014 (-0.181-0.552)	0.141 (-0.280-0.832)

	Global	Low used (N=5119)	Recently used (N=3189)	Steadily used (N=1559)
Industrialization[5]	0.039 (-0.556-0.819)	-0.001 (-0.288-0.296)	0.381 (-0.15-0.819)	-0.011 (-0.556-0.597)
Post-industrializtion[6]	0.004 (-0.278-0.327)	-0.002 (-0.211-0.133)	0.164 (-0.173-0.327)	-0.019 (-0.278-0.293)
Times of remarkable land use [highest number of grid-cells transformed (yr)]				
FU[7] (N=5916)	AD1900	AD1900	AD1900	BC3000
LU_{max}[8]	AD2000	AD2000	AD2000	AD1750
Duration of remarkable land use [median (yr, % time until present)]				
FU	250 (100%)	50 (80%)	100 (100%)	2750 (100%)
LU_{max}	50 (80%)	0 (0%)	0 (0%)	100 (60%)
Value of remarkable land use [median, min-max (portion of grid cell)]				
FU	0.271 (0.200-0.871)	0.234 (0.200-0.477)	0.283 (0.200-0.783)	0.286 (0.2-0.871)
LU_{max}	0.346 (0-1)	0.054 (0-0.52)	0.652 (0.278-1)	0.642 (0.294-0.979)
Mammalian diversity				
Species richness	55 (1-251)	41 (1-251)	63 (1-243)	68 (20-250)
Threatened spp richness	2 (0-40)	1 (0-40)	2 (0-33)	3 (0-32)

[1]BC6000- AD2000; [2]BC6000-AD0; [3]AD0-2000; [4]AD0-1750; [5]AD1750-AD1950; [6]AD1950-2000. [7]First Use, >0.2 human land use per grid cell; [8]Land Use Maximum, maximum human land use per grid cell, considering the whole time series.



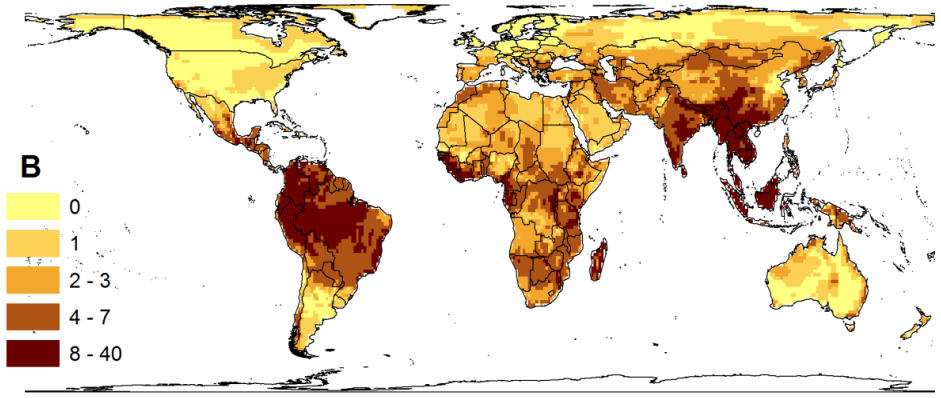


Figure 4.S3. Spatial distribution of total mammalian richness (A) and numbers of threatened mammals (B). Projection: Berhmann cylindrical equal area.

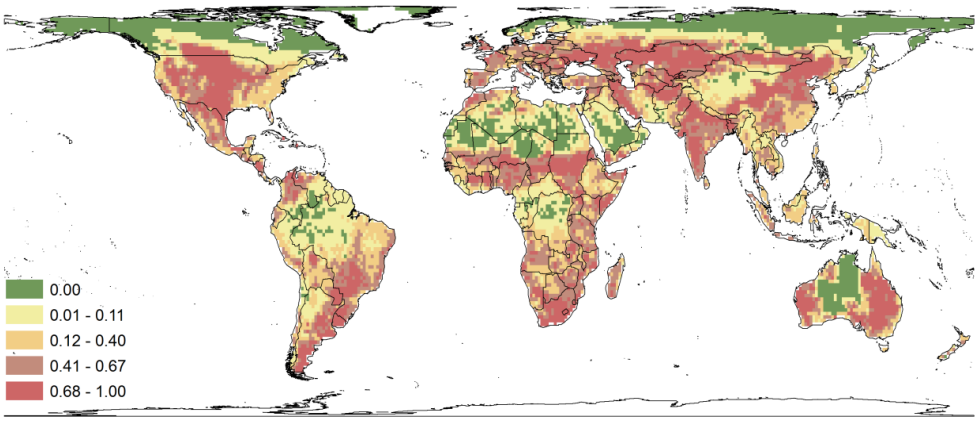
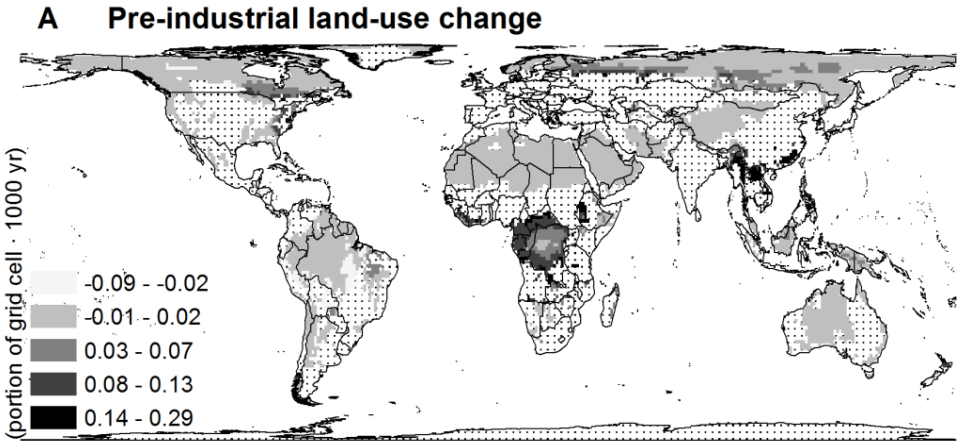


Figure 4.S4. Spatial distribution of portion of present human land use (c.A.D 2000). Projection: Berhmann cylindrical equal area.



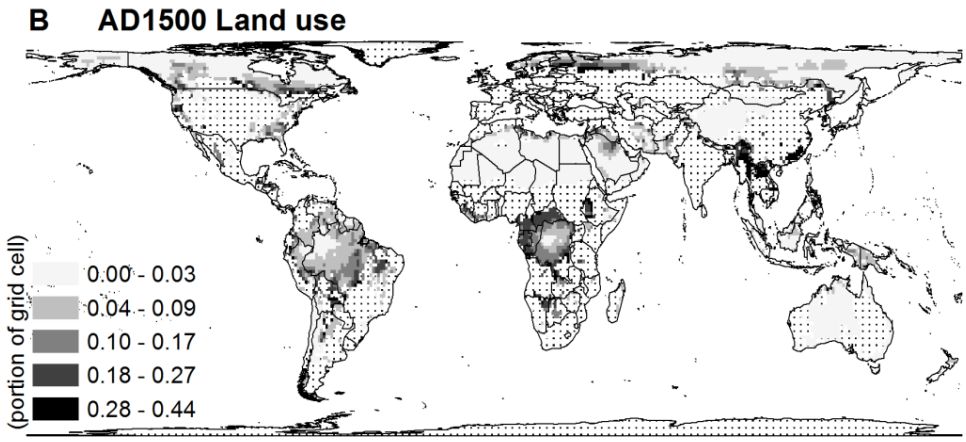
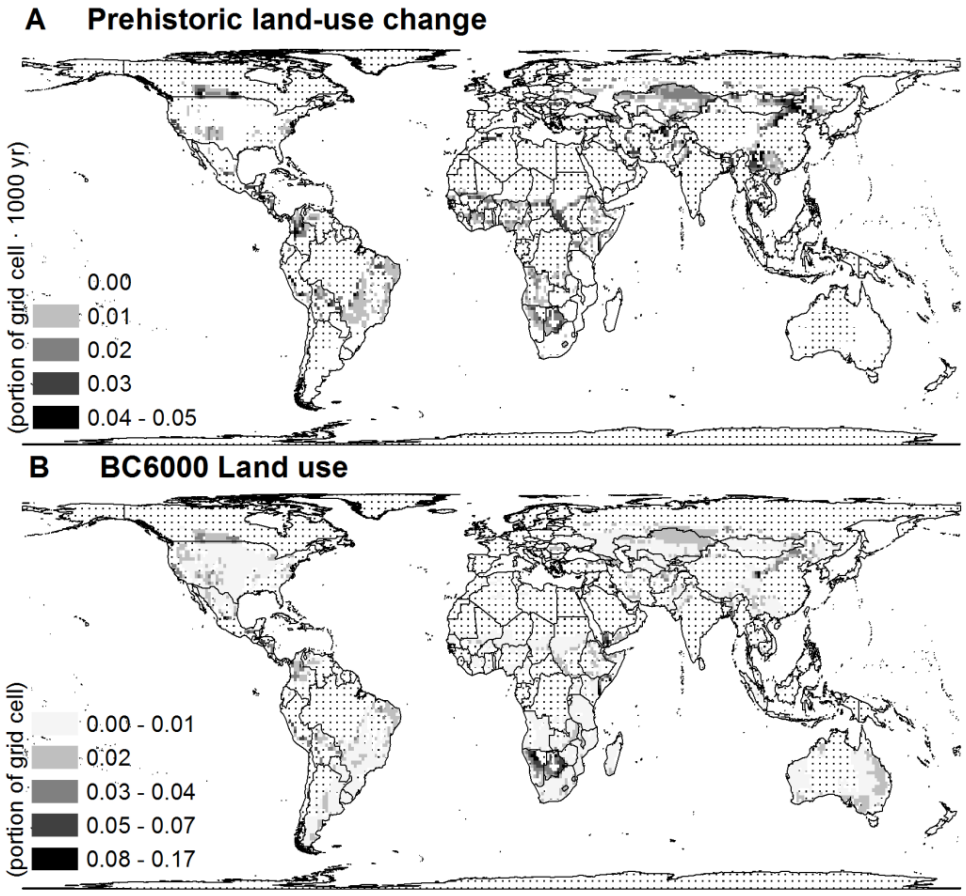


Figure 4.S5. Spatial distribution of relevant past land-use metrics for regions classified as *low-used* areas. Rate of land-use change for the pre-industrial period (A), relevant to explain both threatened and total mammalian richness distribution; and human land use at c.A.D.1500 (B), relevant to explain only total mammalian richness distribution.



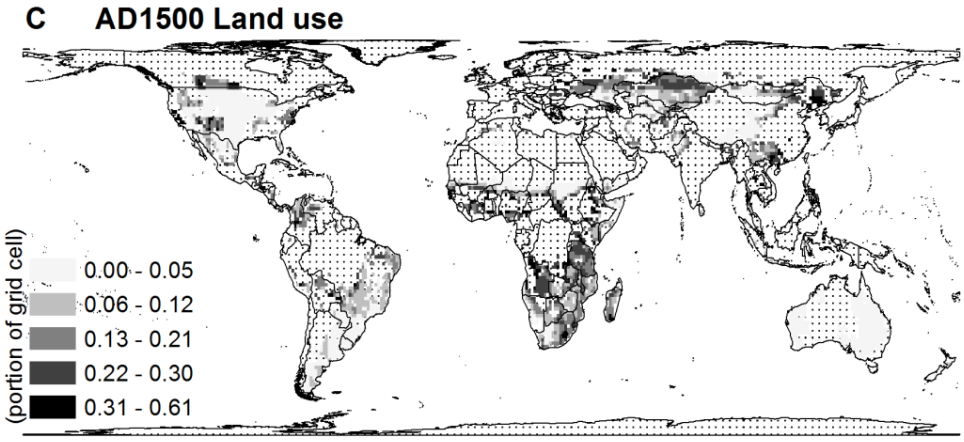


Figure 4.S6. Spatial distribution of relevant past land-use metrics for regions classified as *recently-used* areas. Rate of land-use change for the prehistoric period (A) and human land use at c.B.C.6000 (B), relevant to explain threatened mammalian richness distribution; human land use at c.A.D.1500 (C) relevant to explain total mammalian richness distribution.

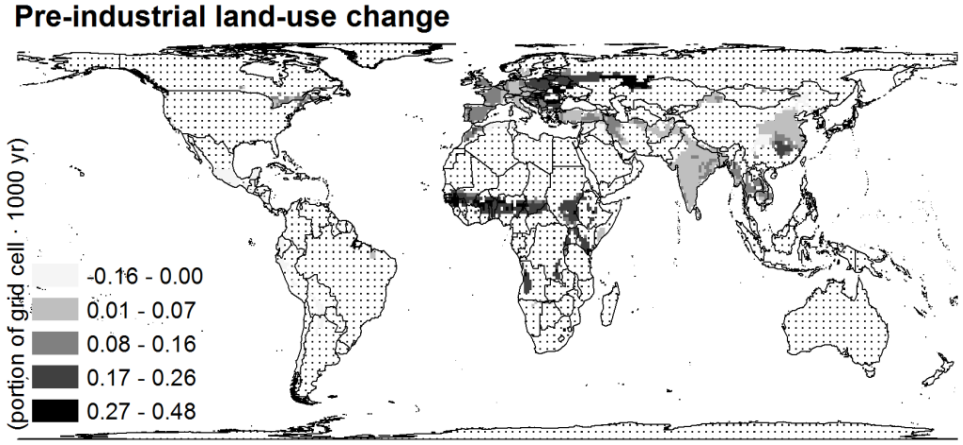


Figure 4.S7. Spatial distribution of relevant past land-use metrics for regions classified as *steadily-used* areas. Rate of land-use change for the pre-industrial period, relevant to explain threatened mammalian richness distribution.

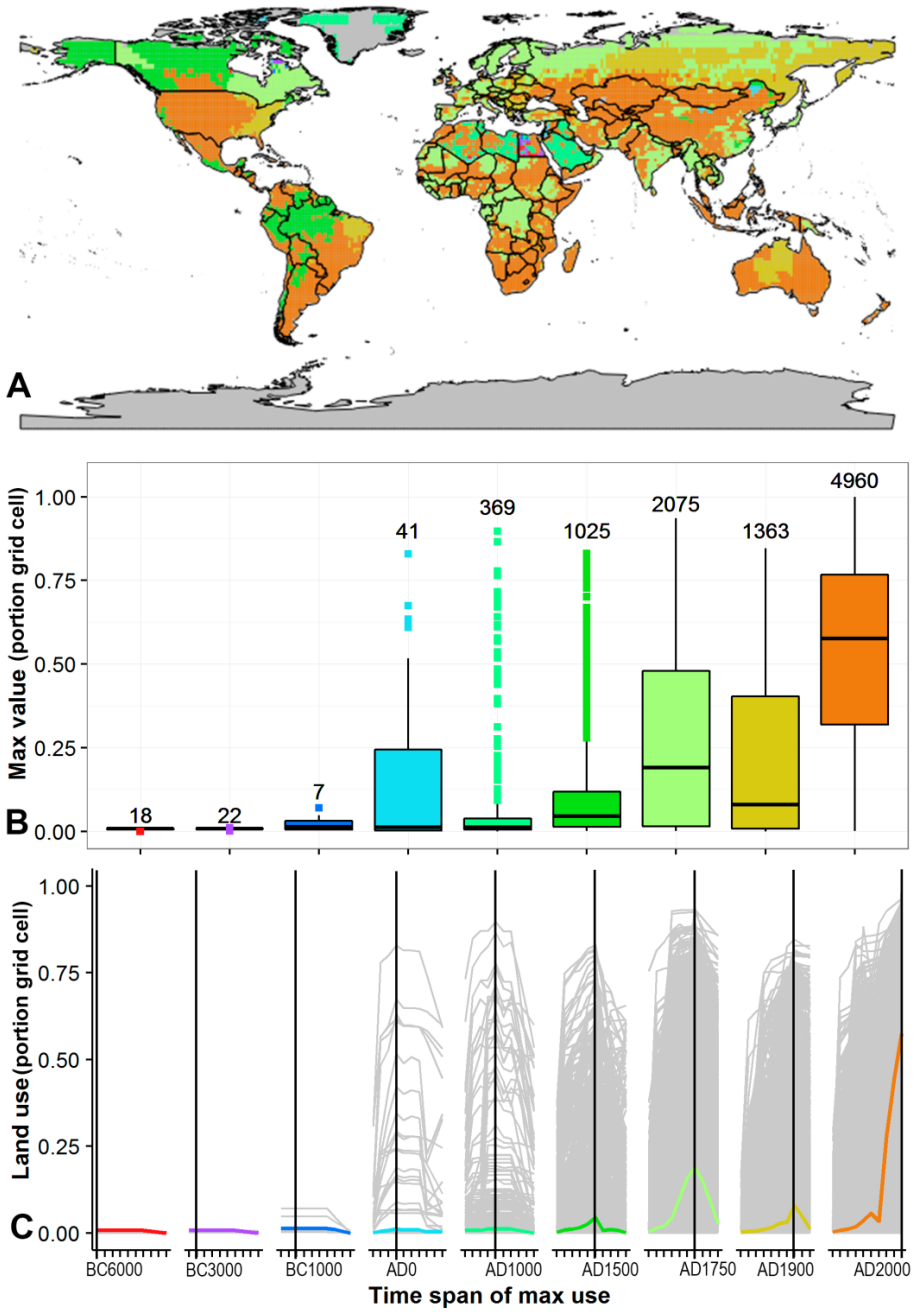


Figure 4.S8. Summary of maximum land use (LU_{max}) per grid cell, according to the KK10 model. Color legend and main Y axis show different LU_{max} time spans, as in panel C (none grid cell presented a maximum value in the period A.D. 1950). Panel A maps areas according to their LU_{max}; grey-colored grid cells are not included in the KK10 model or have areas lower than 10,000 km^2. Panel B shows the actual LU_{max} value (portion of grid cell; Y axis); numbers above boxes refer to the number of grid cells which achieved the LU_{max} in that time span. Panel C represents the individual (grey) and median (colored) trajectories of grid cells along the whole time series (B.C.6000-A.D.2000, minor-X axis), vertical black lines marking LU_{max} time; Y axis displays the percentage of used land (% of grid cell).

Appendix 4.S3. Additional information of the within trajectory-cluster analyses (BRT).

Key concept of boosted regression trees (adapted from Elith et al. 2008)

Parameters

Bag fraction: It specifies the proportion of data to be selected at each step, before a split is made.

Tree complexity: It controls whether interactions are fitted, and how many of them should be considered. It represents the number of nodes in a tree, e.g. a value of 1 indicates a single decision stump, with two terminal nodes.

Learning rate: (also shrinkage parameter) It determines the contribution o each tree to the growing model. The lower the value of this parameter, the higher the number of trees necessary to fit the model.

Outputs

Variable importance: It is based on the number of times a variable is selected for splitting, weighted by the squared improvement to the model as a result of each split, and averaged over all trees. The relative influence (or contribution) of each variable is scaled so that the sum adds to 100, with higher numbers indicating stronger influence on the response.

Number of trees: BRT is based on boosting method, which is based on the idea that it is easier to find and average many rough rules of thumb, than to find a single, highly accurate prediction rule. Therefore, many trees are tried and then averaged weighted by the learning rate. When using *gbm.step* function, there is no need to fix the number of trees *a priori,* because the algorithm tries to minimize the predictive deviance and calculates the optimal number of trees by cross validation. A minimum of 1000 is advised to obtain confident results; thus if not achieved, a smaller learning rate should be fixed.

Explained deviance: Consider a loss function (here deviance) that represent the loss in predictive performance due to a suboptimal model. Boosting is a numerical optimization technique for minimizing the loss function by adding, at each step, a new tree that best reduces the loss function. Thus, explained deviance is the amount of deviance that the model has achieved to explain, where the null deviance is the initial value before any split is made.

Table 4.S2. Results from the BRTs global and by trajectory-cluster (*low, recently and steadily used*) including 'null-model' variables and past land-use indicators (past land use, rates of land-use change, remarkable land use and duration of first use). Two response variables were explored, number of threatened mammals and total mammalian richness. *Variable importance* quantifies the effect of each variable on prediction. *Number of trees* is the optimal number over which final results are drawn. *Explained deviance* is the model explanatory power, respect to the null deviance is the initial value before any split is made.

Variable importance	Threatened				Total richness			
	Global	Low	Recently	Steadily	Global	Low	Recently	Steadily
Null model								
Latitude	12.61	11.23	10.15	18.40	55.79	69.32	42.81	49.12
Total richness	46.06	51.35	38.44	30.90	-	-	-	-
Present LU_{AD2000}	0.67	1.99	0.58	1.68	0.38	0.35	0.38	0.49
RAC[1]	15.47	10.81	15.45	8.36	20.55	8.72	24.54	25.84
Trajectory-cluster	0.02	-	-	-	0.00	-	-	-
Past land use								
BC6000	1.26	1.05	8.62	3.06	0.79	0.61	2.26	1.21
BC3000	0.32	0.27	1.20	1.72	0.10	0.14	0.61	0.64
BC1000	0.39	0.28	1.08	0.83	0.10	0.07	0.57	0.74
AD0	0.49	0.38	1.56	0.67	0.12	0.15	0.60	0.37
AD1000	0.46	0.53	1.01	0.76	0.25	0.16	0.94	0.55
AD1500	4.97	5.02	3.00	1.00	7.76	6.83	12.57	1.07
AD1750	0.61	1.12	1.08	0.78	0.40	0.71	0.68	4.76
AD1900	1.14	1.10	1.61	2.78	2.10	1.79	0.66	2.51
AD1950	0.50	0.73	2.03	1.42	0.21	0.16	0.49	0.57
Rates of land-use change								
Prehistoric[2]	4.29	2.52	8.65	1.87	0.58	0.48	3.42	4.89
Pre-ind.[3]	7.58	5.59	2.42	19.11	6.50	6.35	5.11	4.04
Industrialization[4]	1.06	1.59	1.47	3.35	0.20	0.38	0.76	0.80
Post-ind.[5]	0.76	3.70	1.01	1.01	0.30	0.19	2.95	0.64
Remarkable land-use change								
LU_{max}	0.23	0.46	0.55	1.93	0.97	0.82	0.58	1.12
FU[6] duration	1.12	0.29	0.07	0.38	2.88	2.76	0.08	0.62
No. trees	10500	9200	11250	6800	6600	5000	7550	5150
Explained variance	90%	92%	84%	86%	96%	96%	91%	88%

[1]Residual autocovariate; [2]BC6000-AD0; [3]AD0-1750; [4]AD1750-1950; [5]AD1950-2000; [6]FU, first significant use (>0.2 grid cell used by humans).

General discussion

Zonification complements spatial conservation planning by prioritizing actions instead of areas

Untangling the main causes of vulnerability to extinction may be tackled from two broad points of view: the species (or any other taxonomic unit) or the spatial level. **Comparative extinction risk studies** are the main source of knowledge on the intrinsic bases that predispose species to extinction (e.g. Davidson et al. 2009). The tradition in this approach is already long and has given rise to numerous debates, including the questioning of its applicability and usefulness for conservation policy (Cardillo & Meijaard 2012); but also to great advances in the holistic comprehension of species' traits associated to a greater risk of extinction, pointing to general processes that may be common to many of them. This type of studies can sometimes seem too simplistic, since it is not possible to separate the nature of threatened species from the threatening process itself as these can strongly interact (González-Suárez et al. 2013). Thus it is necessary to further include information on external threats to complete many of the general rules obtained from comparative extinction risk studies (Murray et al. 2014). Anyhow, results are relatively consistent within taxonomic groups (Verde Arregoitia 2016) and have proved applications beyond priority ranking of species (Cardillo et al. 2006; Di Marco et al. 2012). In Chapter 1 we have shown an additional application of this type of studies which does not require an exhaustive number of predictors of vulnerability and that could be extended to additional groups and subgroups of species, or implemented more locally at continental or even regional scales. Tools like this are a crucial step towards the synthesis of the overwhelming amount of information that is becoming available globally.

An area can be susceptible in many senses including multiple facets within the spatial (species composition and interactions, environmental conditions, topography, human activities, etc.) and the temporal domain (past species composition, environment, etc.). The literature on spatial conservation planning has focused on preserving the maximum of a given natural value (vulnerability, irreplaceability, total or functional diversity, etc.) with the minimum invested resources (land, money, etc.; Margules & Pressey 2000; Joseph et al. 2009; Moilanen et al. 2011). Designing the optimal network of protected areas must be a goal of conservation biology, despite

being hard to achieve. However, complementary approaches, based on **prioritizing actions according to the attributes of a given area** (Chapter 1), may help preserve natural values using a wider range of approaches going beyond the delimitation of protected areas, a conservation action that is not always feasible and may not always be effective.

Transboundary threats and the myth of developed countries as environmentally concerned

As previously discussed, within the spatial domain many factors contribute to shape the distribution of current diversity and more specifically, of vulnerable species. Beyond the proximate causes that threat and remove biodiversity (e.g. habitat loss, introduction of non-native species, hunting), there is a whole human context which involves many decisions that are the ultimate roots of nature conservation success. Additionally, the socioeconomic context determines the type of human activities that take place within a given area and, therefore, the potential damages to which natural systems are exposed.

Many preconceived ideas exist about the areas where most endangered species and ecosystems occur. Most mammals inhabit tropical latitudes because environmental particularities have generated higher diversity in these areas (Schipper et al. 2008), but also because these regions still have patches of natural habitats where sensitive species are able to persist (Chapter 3; Sanderson et al. 2002). A closer look to the socioeconomic profile of these areas reveals that areas richer in threatened species are rural, with relatively high socioeconomic development and with high values of international exports and low-intermediate values of tourism (Chapter 2). On the other hand, countries without threatened mammals are either European countries or Small Island Developing States (SIDS), socioeconomically disparate countries but likely with a common distant past of human-mediated local extinctions (Ceballos & Ehrlich 2002; Morrison et al. 2007). These findings highlight the importance of **transboundary impacts** and support the view that traditionally developed countries are responsible of great part of the tropical devastation of biodiversity, acting at the

expense of less restrictive legislations (Mandemaker et al. 2011; Lenzen et al. 2012). Additionally, the results emphasize the idea that **the absence of threatened mammals is not necessarily a positive attribute**.

To further explore the role of socioeconomic indicators we clearly need to go beyond the national scale, which often includes very heterogeneous regions and even regulations. However, there is a still a long way to go before disaggregated sub-national data are available for the totality of countries of the world, regardless of their socioeconomic development status (Amano & Sutherland 2013). In the meantime, conducting local studies for areas with available information and global studies as the one presented in this thesis can offer useful insights and highlight the complexities in understanding the role that human play in biodiversity loss.

Different stages of agricultural development show different land-use/threatened species relationships

We normally assume that an increase in the extension, intensity or duration of a human activity on land would negatively impact biodiversity; however, the present work shows actual patterns may be much more complex (Chapters 3 & 4). That assumption may be met at a local or regional scales, considering that these changes on land are normally associated to loss of natural uses (Kleijn et al. 2006; Herzon et al. 2008). However, two important points need to be made here that are particularly relevant when using large spatial units of analysis. First, the possibility of increasing agricultural activities without converting natural habitat exists via improved efficiency of already existing croplands. Higher land-use intensity may not necessarily be linked to additional threats for species and can instead offer a good balance between sustainability and biodiversity persistence ('sparing land'; Foley et al. 2011; Mueller et al. 2012). Second, causality can only be inferred with experimental or in carefully controlled situations which are generally limited to local scales. Most studies of biodiversity changes actually describe patterns, which can vary radically among scales and thus, should be accordingly interpreted. In conclusion, we cannot state that a greater extent, intensity or time of use will not lead to greater impacts for mammals,

but that patterns at a global scale are complex and show non-linear and region-specific relationships.

The existing complexity also became apparent when testing the proposed *refuge* and *threat* hypothesis. First, we show that these two apparently contradictory hypotheses may actually describe different sections of a non-linear relationship between land use and biodiversity. Second, we find that this relationship appears to describe dampening cycles and that we have already moved beyond the initial stages of agricultural development in most of the Earth surface. Only some parts of the Neotropics seem to adjust to the *threat* hypothesis. The rest of realms containing **tropical and subtropical** biomes (namely Afrotropics, Australasia and Indomalay) are rich in ***refuge*** areas, which instead we expected would have been prevalent in more humanized regions. Any additional pressure on these regions will likely cause important biodiversity loss. In more **humanized regions**, like Europe and some areas of the Neotropics, where we may think there is little to worry with no or little biodiversity left, we actually found '***novel' threat*** areas where threatening activities co-occur with likely less sensitive, but now threatened species. The idea of existing *'novel' threat* areas needs to be further tested and raises interesting new questions, such as: Are threatened species of developed countries distinct, less sensitive, from those threatened in developing countries? Have we already lost most of intrinsically vulnerable species? Additional studies including changes through time in biological and ecological traits of species, or ecosystems' properties, will be necessary to further evaluate these intriguing findings.

Not many studies have evaluated the relationship between land-use metrics and species richness' distribution at the global scale, and even fewer have explored such a wide variety of metrics as analyzed in the present thesis (but see Kehoe et al. 2015). One explanation for this may be related to data quality issues. Global diversity distribution is relatively well-known for mammals, amphibians, birds and plants (Edwards et al. 2000; BirdLife International 2015; IUCN 2015), although there is considerably room for improvement (Hortal et al. 2014; Meyer et al. 2016). Several of the land-use databases analyzed here were only recently made available (e.g. Ramankutty et al. 2008; Hansen et al. 2013; Siebert et al. 2015), and the conceptual

framework to synthesize this information and make it applicable for different disciplines, including conservation biology, was missing before the big-data era (Erb et al. 2013; Václavík et al. 2013). Despite the questionable quality of some of these sources, getting the best of the available information should be a scientific duty in order to progressively understand global drivers of biodiversity loss.

A closer look to the past reveals a greater relevance of past land-use changes

As multiple disciplines start to be (finally) integrated, increasing evidence shows the relationship between current biodiversity distribution and conservation status and past human pressures (Redman 1999; Faurby & Svenning 2015b; Boivin et al. 2016). However, we show that simple, and thus, apparently appealing, indicators of land-use history (Chapter 3) may not be adequate to reflect historical influences on current patterns of mammals distribution. The final chapter of this thesis offers an extensive analyses of past land use metrics to illustrate their potential value and once again highlight the complexity in understanding biodiversity patterns.

Land-use trajectory classification offers an innovative and straightforward way of integrating temporal series of this type of data, which might be transferred to any spatial scale. This would allow, for example, classifying regions according to their fire regimes or their frequency of land-cover change, and establishing managing units for land-use planning (Boucher et al. 2014). In our case, the separation of land-history trajectories allows to identify potentially important pattern with conservation implications, such as the probable extinction debt within *low*-and *recently-used* areas (Chapter 4). Obviously, the three obtained groups of areas depend on the analyzed data and data on past land use can be based on different assumptions. Therefore, comparisons with alternative currently available or forthcoming models of past land-use (Goldewijk et al. 2010) would be advisable to further explore how past human actions have affected current biodiversity patterns.

Past land-use indicators play a relatively important role in explaining present biodiversity patterns compared to present land use, a finding also reported by others (Dullinger et al. 2013). In addition, for the areas analyzed the most informative metrics

are related to past land-use extension and rates of change (Chapter 4). Future analyses for different regions would be useful to clarify if indeed extension and rates of change are key descriptors. Interestingly, our findings show that threatened mammals' distribution is more influenced by past human activities than total mammals' distribution. This may be due to the fact that total mammalian richness is predominantly conformed by common and widespread species (Orme et al. 2005; Lamoreux et al. 2006), whose response to anthropization is lower.

Synthesis and future perspectives

During the course of human history, many factors have contributed and still contribute to the current conservation status of biodiversity at the global scale. In this PhD thesis I have looked at indicators measurable today from the species point of view, regarding species nature (*How are the most endangered species like and where are they located?*); but mainly have considered the spatial perspective, i.e. human activities that threaten biodiversity (*Which land uses are associated to more threatened species?*) and the socioeconomic context (*Which are the socioeconomic features that predispose areas to harbor threatened species?*). In addition, indicators related to past conditions, focusing on land use, were explored (*Can the inclusion of past land-use indicators improve our understanding of present species richness? Which metrics are more appropriate to evaluate these patterns?* Fig. D.1). Additional factors, especially those related to climatic conditions (abiotic factors, Fig. D.1), could be included to complete our comprehension of global distribution of vulnerability (vulnerability due to climate change, for example), both from the perspective of current conditions, and by exploring past trajectories to forecast future conditions. Moreover, other factors from the past have remained unexplored, such as past socioeconomic conditions, or the change of ecological/life-history traits of species through time (Fig. D.1). Jointly studying past and present complex and interconnected conditions of systems is not an easy task, although is becoming more feasible improved tools and integration of data from multiple disciplines.

Studying the relationship between humans and biodiversity along the temporal succession of human expansion and development is very complicated as data are not available for long temporal windows. Alternative we can make a strong assumption and explore this relationship by looking at different regions of the world within a single temporal window (present), and considering that these regions represent different steps within the temporal succession. Although this can give us an idea of broad patterns, it must be noticed that trajectories that have led to the current situation are variable and may have occurred at different paces. Thus, recent abrupt changes may have greater impacts than longer-term steady small changes along which some species would have had time to adapt to human presence. Nevertheless, this type of exercise can help in improving our conceptual understanding of how patterns and processes relate along the current biodiversity crisis.

Studies at the global scale should aim towards the creation of a general framework that allows comparing very different areas and species and accounts for the distinct conservation problems faced in different places. Working at the global scale is also a big responsibility, because interpretations may lead to general opinions and oversimplifying assumptions which may be difficult to later correct. Global approaches must not be regarded as offering direct conservation tools for managers, but instead as guides that provide general understanding and the means to identify potential shared policies across the world. Hopefully, this work has contributed to these goals in the right direction.

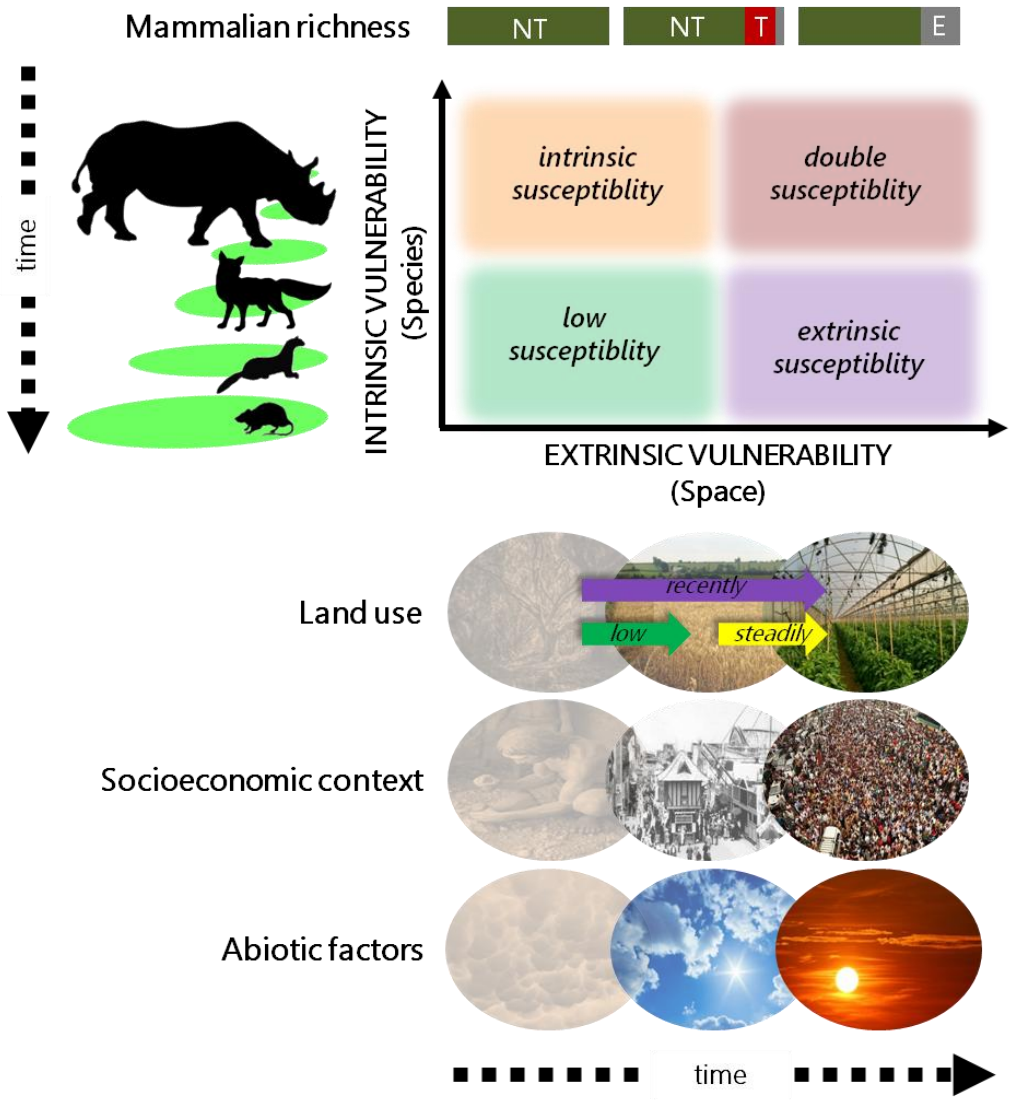


Fig D.1. Synthesis of the multiple relationships between extrinsic factors (associated to space); intrinsic factors (associated to species) explored in the current PhD and those that could be explored in the future. Mammalian richness legend: *NT* (green), no-threatened; *T* (red), threatened; *E* (grey), extinct.

Conclusions / Conclusiones

Conclusions

- Based on terrestrial mammals' ecological/life-history traits (intrinsic factors) and human land use within their geographic ranges (extrinsic factors), we are able to detect four types of area: *double-susceptibility* areas, where both vulnerabilities are high; *intrinsic-susceptibility* areas, where intrinsic vulnerability is high and extrinsic is low; *extrinsic-susceptibility* areas, where extrinsic vulnerability is high and intrinsic is low; and *low-susceptibility* areas, where both vulnerabilities are relatively low.

- *Double-susceptibility* areas occur primarily in Southeast Asia, Madagascar and Sub-Saharan Africa. *Intrinsic-susceptibility* areas are primarily located in the Sahara region, Botswana-South Africa, Tibet and near the Arctic in the American continent. *Extrinsic-susceptibility* areas occur in most of Europe, North America, Brazil and parts of southern Africa. *Low-susceptibility* areas are essentially found in Siberia and small regions of Europe, North and South America.

- *Extrinsic-susceptibility* areas cover the greatest extent of the globe comparing to the rest of areas, followed by *double-susceptibility* areas when all terrestrial mammals are considered together. This finding highlights the omnipresence of humankind and the declining trend of typically vulnerable species across the world, which are nearly absent from most part of the Earth surface.

- Absence of threatened mammals at the country scale is normally a result of past intense human impacts, which caused the disappearance of the most sensitive species. In general, these countries without threatened mammals are northern European countries or small island developing states (SIDS), with intermediate-high degrees of socioeconomic development.

- Countries harboring more threatened mammals have rural populations and a great dependency on international trade. This suggests that most of threats to which species are exposed have a transboundary origin.

- Human land-use extent, particularly the remaining portions of relatively natural uses within humanized areas, appears as an important factor to understand the distribution of threatened mammals. Land-use intensity metrics complement the understanding of complex relationships between human land use and biodiversity.

- We propose two hypotheses to classify areas according to their relationship between human land use and numbers of threatened mammals. *Refuge* areas, where more threatened species concentrate in relatively little modified zones; and *threat* areas, where more threatened species co-occur with highly modified areas. Our results support both hypothesis and add an additional type of area, *'novel' threat* areas, where threatening activities and threatened species coexist, although they are not located in regions of incipient agricultural development.

- Different biogeographic realms present *refuge* and *threat* areas where threatened mammals concentrate. These patterns relate to the stage of (agricultural) development within each realm. *Refuges* tend to be present in the Tropics, and *threat* areas are almost absent from the whole land surface that has undergone any agricultural modification. On the other hand, *'novel' threat* areas must not be overlooked; they are mainly located in Europe, where it will be possible to observe new mammalian declines and local extinctions.

- According to their trajectory of land use, we define three types of areas, *low-used* areas, where land-use values are low, with small increases in use over time and moderate declines at present. *Recently-used* areas present moderate rates of land encroachment until relatively recent times (~A.D.1750), when a strong increase in human land use can be observed. In *steadily-used areas,* the initial land use was higher than in the rest of trajectories and increased at a relatively constant rate, with a soft steepening around B.C.1000 and a moderate recent decline.

- *Low-*, *recently-* and *steadily-used* areas do not present significant differences in total or threatened mammalian richness, but differ in the type of relevant metrics

and temporal periods explaining total and threatened mammalian richness distribution.

- Past land-use indicators are overall more relevant than present land use to explain total and threatened mammals distribution. Particularly rates of change and portion of land use prior to the Industrial Revolution appear as relevant in most of the land surface.

Conclusiones

- En base a los rasgos de historia de vida/ecológicos de los mamíferos terrestres (factores intrínsecos) y a los usos del suelo humanos que tienen lugar dentro de su rango de distribución (factores extrínsecos), podemos detectar cuatro tipos de área: áreas de *doble susceptibilidad*, donde ambas vulnerabilidades presentan valores altos; áreas de *susceptibilidad intrínseca*, donde la vulnerabilidad intrínseca es alta y la extrínseca es baja; áreas de *susceptibilidad extrínseca*, donde la vulnerabilidad extrínseca es alta y la intrínseca baja; y áreas de *susceptibilidad baja*, donde ambas vulnerabilidades son relativamente bajas.

- Podemos encontrar áreas de *doble susceptibilidad* en el Sudeste Asiático, Madagascar y el África subsahariana. Las áreas de *susceptibilidad intrínseca* se concentran fundamentalmente en la región del Sáhara, Botswana-Sudáfrica, Tibet y cerca del Ártico en el continente americano. Las áreas de *susceptibilidad extrínseca* se sitúan en gran parte de Europa, Norteamérica, Brasil y ciertas partes de África del sur. Las áreas de *baja susceptibilidad* se encuentran sobre todo en Siberia y en pequeñas regiones de Europa, Norte y Sudamérica.

- Las áreas de *susceptibilidad extrínseca* cubren la mayor extensión del globo en comparación al resto de áreas, seguidas de las de *doble susceptibilidad* (considerando todos los mamíferos terrestres). Este resultado destaca la omnipresencia del ser humano y la tendencia decadente de las especies típicamente consideradas vulnerables a lo largo y ancho de nuestro planeta, las cuales se encuentran casi ausentes de la mayor parte de la superficie terrestre.

- La ausencia de mamíferos amenazados a nivel de país normalmente es resultado de un pasado de intensa actividad humana que causó la desaparición de aquellas especies más sensibles. En general, estos países sin mamíferos amenazados son países del norte de Europa o pequeños estados insulares en desarrollo (SIDS), con estadios de desarrollo socioeconómico medio-alto.

- Aquellos países que contienen un mayor número de mamíferos amenazados tienen poblaciones rurales y una gran dependencia del comercio internacional. Esto sugiere que la mayoría de amenazas a las que se ven expuestas las especies tienen un origen transfronterizo.

- La extensión del uso del suelo humano, particularmente las porciones remanentes de usos relativamente naturales dentro de áreas humanizadas, aparece como un factor importante para entender la distribución de los mamíferos amenazados. Indicadores de intensidad de uso complementan la comprensión de las complejas relaciones entre el uso del suelo humano y la biodiversidad.

- Proponemos dos hipótesis para clasificar áreas de acuerdo a su relación entre uso del suelo humano y número de mamíferos amenazados. Áreas de *refugio,* donde las especies amenazadas se concentran en zonas relativamente poco modificadas; y áreas de *amenaza,* donde las especies más amenazadas se encuentran en áreas ampliamente modificadas. Nuestros resultados apoyan ambas hipótesis y añaden un tipo de área adicional: las áreas de *'nueva' amenaza*, donde actividades amenazantes y especies amenazadas coinciden, aunque no se encuentran en regiones de incipiente desarrollo agrícola.

- Distintas regiones biogeográficas presentan áreas de *refugio* y de *amenaza* donde los mamíferos amenazados se concentran. Estos patrones tienen que ver con el estado de desarrollo (agrícola) de cada una de estas regiones. Los *refugios* tienden a encontrarse en los Trópicos, y las áreas de *amenaza* se encuentran prácticamente ausentes de la superficie terrestre que ha sufrido algún tipo de modificación agrícola. Por otro lado, las áreas de *'nueva' amenaza* no deben pasarse por alto; se encuentran principalmente en Europa, donde será posible observar nuevos declives y extinciones locales de mamíferos terrestres.

- De acuerdo a su trayectoria de uso del suelo, definimos tres tipos de áreas: *poco usadas*, donde los valores de uso del suelo son bajos, con pequeños aumentos en el uso a lo largo del tiempo y declives moderados en la actualidad. Las áreas *recientemente usadas* presentan tasas de uso del suelo humano moderadas hasta

tiempos relativamente recientes (~1750 A.D), cuando se observa un fuerte incremento del uso humano. En las áreas *continuadamente usadas* el uso del suelo inicial fue más alto que en el resto, su tasa de crecimiento se mantuvo constante hasta entorno el 1000 A.C., cuando se produjo un cambio brusco, y presentan un declive reciente moderado.

- Las áreas *poco*, *recientemente* y *continuadamente* usadas no presentan diferencias significativas en cuanto a riqueza total o de mamíferos amenazados, pero se diferencian en el tipo de indicadores y los periodos temporales que son relevantes para explicar la distribución de mamíferos totales y amenazados.

- Los indicadores de uso del suelo pasado son, en términos generales, más relevantes que el uso presente a la hora de explicar la distribución actual de mamíferos totales y amenazados. Concretamente, las tasas de cambio y la proporción de uso anteriores a la Revolución Industrial son relevantes en gran parte de la superficie terrestre.

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Porque no hay imposibles... sólo improbables.

This PhD thesis explores how different **anthropogenic factors** influence the distribution of mammalian species at a global scale, especially of those more endangered. The socioeconomic context of a country, the extent and intensity of human land use, now and in the past; along with particular species' traits, make some areas of the world more vulnerable to extinction. The identification of such factors allows detecting the major conservation problems of each region and designing more effective strategies to guarantee their preservation, according to the particularities of each zone.

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